PHYLOGENETIC PATTERNS AND HYBRIDIZATION[1]

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ABSTRACT

Hybridization is an important part of the evolutionary history of flowering plants. If hybridization has occurred among the species of a taxon under cladistic analysis the results are varied but always present additional difficulties. Hybridization results in incongruent intersecting data that obscure the underlying hierarchy. Guidelines and methods are examined for their usefulness in identifying possible hybrids in a cladistic study. Seven genera are analyzed cladistically and the resulting cladograms examined for possible hybrids. These hypotheses of hybridization are then compared to other data, such as distribution and cytology, to see if the hypotheses of hybridization are supported or rejected. The more hybrids an analysis contains and the more complex the interactions, the more difficult it becomes to identify possible hybrids and their parents.

It is difficult to overemphasize the importance of hybridization and polyploidy in evolution because they are outstanding features of many plant groups. According to some authorities 30–80% of the species of angiosperms are polyploids (Goldblatt, 1979; Lewis, 1979; Stebbins, 1974), which allows for the possibility of a tremendous amount of hybridization. Of course, these figures do not include diploid hybrids. Despite its importance, hybridization has been virtually ignored by those who have dominated the discussion of evolutionary theory. This is a result, no doubt, of evolutionary theory being largely in the hands of scientists who work on groups in which such phenomena as polyploidy and hybridization have a strong relationship with unisexuality and are not considered important in evolution.

There are different types of hybridization. Figure 1 summarizes some of the possibilities (a more detailed explanation is found in Funk, 1981) but does not include introgression. For the purpose of this paper it is important to note that many hybrids are sexually reproducing individuals and are morphologically distinct and in some manner reproductively isolated from both parents. Thus, they behave as species no matter whose definition you chose to adopt.

THE STUDY OF HYBRIDIZATION

The basic concept of phylogenetic systematics (sensu Hennig, 1966) is an ever branching pattern or hierarchy. The method of cladistics (phylogenetic systematics) seeks to discover these patterns by grouping together taxa that share apomorphies (evolutionarily novel, unique, or derived characters). Hybridization, or reticulate evolution, is inconsistent with a method designed to depict hierarchies. Hybridization is, therefore, a cause of incongruent, intersecting data that obscure phylogenetic information. Cladists have been concerned with this problem for several years. Most realize that any method that seeks to identify patterns of relationship must be able to accommodate hybridization because of its frequency. Workers in the problems of hybridization and phylogenetic systematics include Bremer (1983), Bremer and Wanntorp (1977), Clark (1982), Funk (1981), Humphries (1983), Humphries and Funk (1984), Nelson (1983), Nelson and Platnick (1980), Rosen (1979), Wagner (1969, 1983), Wanntorp (1983), and Wiley and Brooks (1982).

One favorite method of botanists in estimating the closeness of relationships among taxa is the percentage of hybridization in crossing studies. An important point about such hybridization studies was made by Rosen (1979: 277): "reproductive compatibility is a primitive attribute for the members of a lineage and has, therefore, no power to specify relationships within a genealogical framework." We cannot use the ability of two or more species to hybridize as an indication of close relationship because the ability is rela-
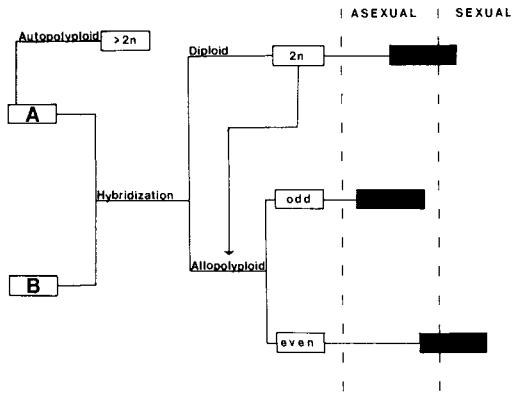
FIGURE 1. Possible hybrid and polyploid relationships of two species (A and B) and their reproductive capabilities (Funk, 1981).

tively ancestral, possessed at one time by all members of the group. In fact, it is the loss of the ability to hybridize that is apomorphic. Because it is never certain that any two taxa are unable to reproduce, whether or not species hybridize is uninformative in determining the pattern of relationship.

Among cladists, three different approaches have been suggested for dealing with the problem of hybridization (Humphries & Funk, 1984). Some suggest using the most parsimonious cladogram(s) and leaving the homoplasies (characters appearing more than once on the cladogram) resulting from the presence of hybrids as the true reflection of the character pattern. Others have advocated removing the hybrids that have been identified by their 'intermediacy' at the beginning of the analysis. The third group advises leaving all of the taxa in the analysis and then closely examining the cladograms for polytomies (nodes with more than two branches) and character conflicts that may indicate possible hybrids. There are problems with all three approaches. The first does not accurately reflect the character pattern; as we shall see, hybrids may appear on the cladogram in a polytomy or with character conflicts or even as ancestors when they are none of these. The patterns do not reflect the accurate sister-group relationship (nor are they true representations of phylogeny). The second approach assumes one can identify the hybrids prior to the analysis and this is not possible in many cases. The third position relies to a great extent on hybrids causing polytomies. Further analysis has shown this usually does not happen (Humphries, 1983).

Wagner (1983) has suggested a method for dealing with hybrids that he calls reticulistics. This method works with groups in which hybrids are intermediate in character and progressively less well with those that are not intermediate. Often the hybrids to which Wagner refers are F_1's that are being formed continually and are sexually inviable. Certainly for well-defined plant groups in which the hybrids are intermediate and obvious and are characterized by being rare and either sterile or polyploids (definition, Wagner, 1983: 71), Wagner's method should be considered. These individuals are not units of evolution and thus are not species. In this paper I am concerned with hybrids that are regarded as evolutionary units and that are usually designated as species, subspecies, or varieties.

Theoretically, in cladograms, hybrids show up by causing character conflicts; so also do homoplasies (Fig. 2, character 4; Appendix A). One must be diligent in trying to distinguish between character conflicts caused by hybridization and those that are the result of parallel or convergent evolution. It is advisable to use the cladogram (developed with the concept of parsimony using all taxa) to examine the apomorphies that appear more than once on the cladogram (homoplasies). Perhaps a closer examination will reveal that some characters originally thought to be apomorphies are actually different structures (false homologies) or are combinations of characters. For instance, not all black anthers in the Compositae genus *Montanoa* Cerv. are homologous. Although originally treated as one apomorphy (Funk, 1982) a close examination showed that some black anthers were black only around the edges of the thecae, some were black only on the top of the connective, while others were completely black. This additional information indicated that "black anthers" was not a single apomorphy but three apomorphies. Character conflicts can also be the result of a designated apomorphy actually containing several characters. Characters such as habit, chromosome number, and flower regularity, all can be divided into several characters. New apomorphies can be added to the cladistic study to reflect the additional information because the "groups of characters" should not be viewed as character conflicts but rather as separate apomorphies. Such changes should be made only when available evidence indicates that they are not homologous. Remaining character conflicts are the result of either undetected homoplasy or hybridization.
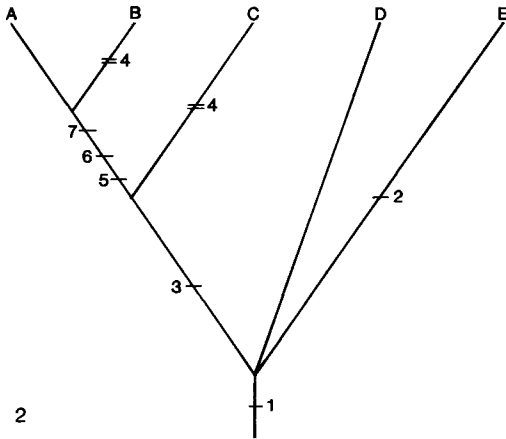
FIGURE 2. Cladogram illustrating character conflict that can be the result of either hybridization or parallel evolution.

A lack of apomorphies can also be caused by hybridity. The hybrid does not necessarily inherit all of the apomorphies of both parents. This observation is important: there is no reason to assume that all apomorphies are dominant over the more plesiomorphic characters of a transformation series. The data presented later in this paper indicate that in the heterozygous condition of the hybrid there might well be a higher percentage of plesiomorphic characters showing in the phenotype. Therefore, it is possible for the hybrid to show only plesiomorphies (primitive, ancestral, or more general characters) and appear on the cladogram in an ancestral position. In Figure 2, taxon D could be a hybrid, between taxon C and any other taxon, that inherited the plesiomorphies of both parents. Indeed, it is interesting to speculate on whether or not one could use such cladistic studies to identify interesting genetic problems.

Often the hybrids in a cladistic analysis will be grouped with one or the other of the parents depending on with which parent they share the most apomorphies (Humphries & Funk, 1984). When the putative parents are sister species (two species that are more closely related to one another than they are to any other species), hy-
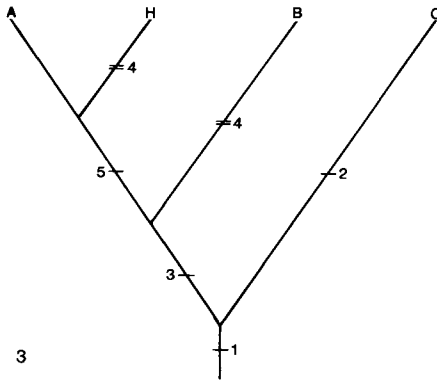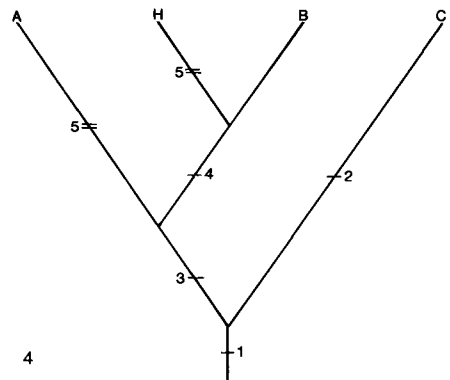
FIGURES 3–6. Cladograms illustrating the pattern of species A and B and their hybrid, H.

FIGURE 7. Cladogram illustrating the pattern of species A and B and their hybrid, H.

brids are quite often apparent regardless of whether or not they form polytomies. Hybrids that form dichotomous branching patterns can be identified as such so long as they have at least one apomorphy of both parents or if they lack an autapomorphy of the parent with which they are grouped. For instance in Figures 3–5 (for characters see Appendix B), species A and B hybridize to g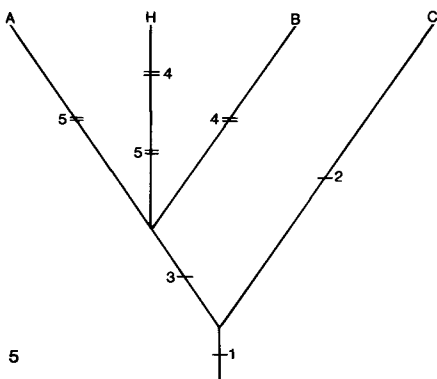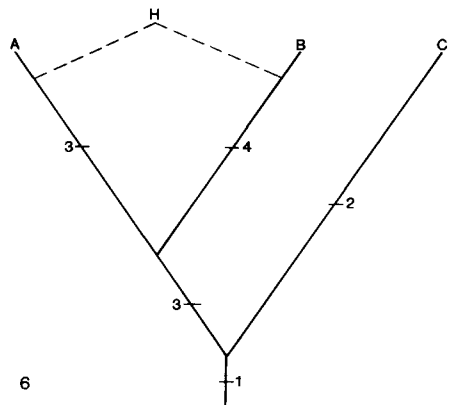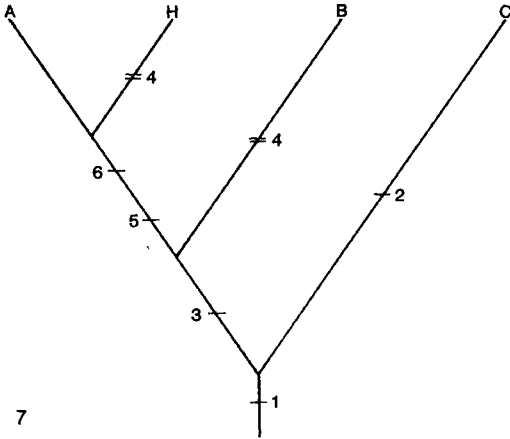ive species H. If there were an equal number of apomorphies in A and B (characters 4 and 5) and if both were found in the hybrid, the result could be expressed as two equally parsimonious cladograms (Figs. 3, 4) or as a trichotomy (Fig. 5), although the latter involves one more character change and is therefore one step longer. If the incongruent character set is inferred to be the result of hybridization, the hybrid could be placed above the diagram connecting with both parents (Fig. 6). However, if one parent taxon had one more autapomorphy than the other, or if the hybrid showed unequal character inheritance, then a single cladogram results. For instance, if taxon A (Fig. 7; Appendix C) had two autapomorphies (5 and 6), and the hybrid inherited all apomorphies of both parents, the most parsimonious cladogram would give the result shown in Figure 7. Nonetheless, because they are sister taxa, the possibility of hybridization is apparent, so long as the hybrid has at least one apomorphy from each parent. However, as mentioned earlier it is possible for the hybrid not to display all the apomorphies. If the hybrid in Figure 7 did not have character 4 there would be no indication that it was a hybrid (except for the

more indirect evidence of lack of apomorphies in taxa A and H). If one parent has very few autapomorphies there is less chance that the hybrid will have any indication of its history.

Sometimes there is more than one hybrid from the same two parents (Figs. 8–12; Appendix D). The two hybrids are most parsimoniously grouped with either parent (Figs. 8, 9) but the two equally parsimonious cladograms indicate the hybridity of H1 and H2. The most parsimonious cladogram has two reticulations (Fig. 12). It is, of course, possible that taxa H1 and H2 are the result of a single hybridization event followed by segregation. One way to evaluate this possibility is to examine the distribution of the taxa in question. The possibility of hybridization followed by segregation lessens as the distance between the hybrid taxa increases.

The only time it is "most parsimonious" to have a polytomy is when the hybrid does not have any of the autapomorphies of either parent (Fig. 13; Appendix E).

However, parent taxa are not always sister taxa. For instance, Wagner (1954) has shown that at least three diploids are involved in producing the hybrids in *Asplenium,* and Grant (1953, 1964) has shown that species from different species groups are hybridizing in *Gilia* (Funk, 1981). In cases such as this the task of identifying hybrids becomes more difficult. For instance, given the cladogram in Figure 14 (Figs. 14–17, 19; Appendix F) the most parsimonious cladogram that includes the hybrid, places the hybrid (H, Fig. 15) as the sister taxon of the parent that involved the least number of homoplasious events (the number of character changes or length of this cladogram is L = 11). The length would increase if the hybrid were grouped with the other parent (Fig. 16, L = 12) because there is one more homoplasy. It is much longer to form a polytomy (Fig. 17, L = 14). The only time a polytomy would be formed in the most parsimonious cladogram is if the hybrid had none of the apomorphies of either parent, at least those above the first node shared by both parents (Fig. 18; Appendix G). If the hybrid is identified as such it can be removed from the cladogram and placed above it giving an even shorter cladogram (Fig. 19, L = 9).

The identification of possible hybrids is only the beginning of an analysis. Those cladograms indicating hybrids (e.g., Fig. 19) are merely hypotheses of hybridization and should be tested by using other data, such as distribution, chro-
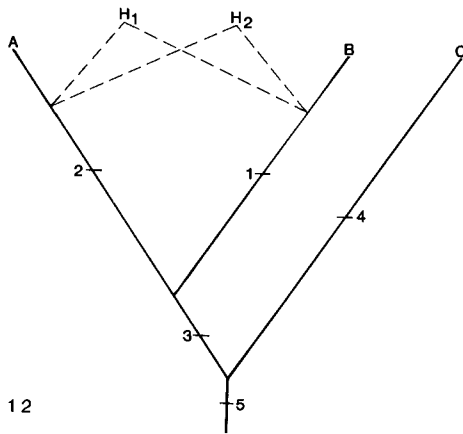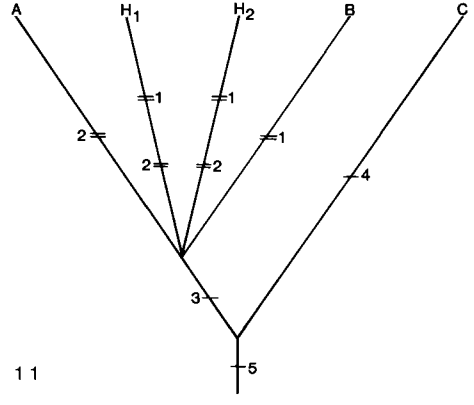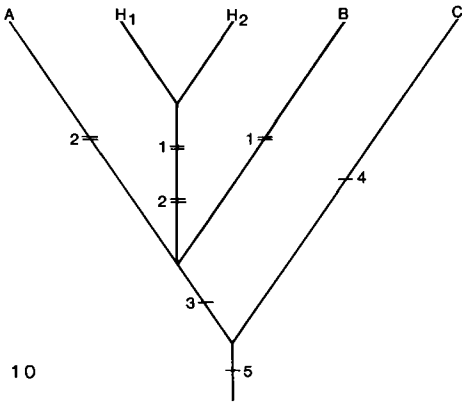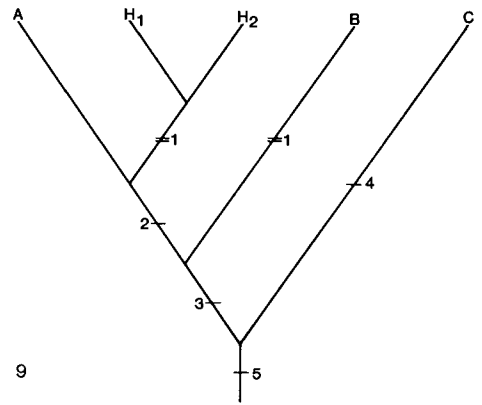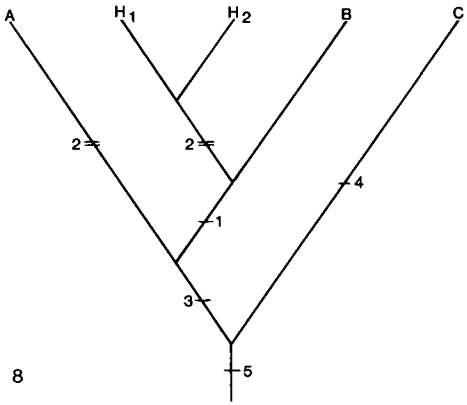
FIGURES 8–12. Cladograms illustrating some of the results when the same two parent species (A and B) produce more than one hybrid, H1 and H2.

mosome number, karyotyping, and pollen fertility before they can be referred to as hybrids.

Nelson (1983) has suggested a method for analyzing cladograms for possible hybrids. His procedure begins with the most parsimonious cladogram without a reticulation and continues by adding reticulations one at a time so as to minimize character conflict. It is based on the idea that when there are two equally parsimonious ways of representing a homology on a cladogram

FIGURE 13. Cladogram illustrating that it is more parsimonious to have a polytomy when the hybrid does not show any of the autapomorphies of either parent.

one should investigate the possibility of inserting a reticulation. If the reticulation results in a decrease of apparent homoplasy and if the taxon exhibits character conflict of the "intermediate" type, the reticulation can be maintained. For a certain set of data (Appendix H) there are two equally parsimonious cladogram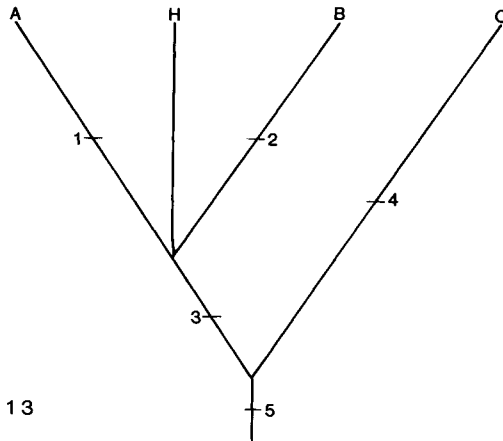s, with the same branching pattern. One cladogram (Fig. 20) has a parallel acquisition of character 4 (Figs. 20–22, Appendix H) and the other has one acquisition of character 4 and a subsequent loss (Fig. 21). However, one can introduce one reticulation and eliminate the need for homoplasy and/or loss (Fig. 22). All this diagram indicates is that *if* hybridization is involved it is most likely that taxon B is of hybrid origin.

A more complicated example involves nine taxa and 12 characters. There are two equally parsimonious cladograms with the same branching pattern with different amounts of homoplasy and loss (Figs. 23, 24; for characters for Figs. 23–25 see Appendix I). By progressively adding reticulations, all need of reversal and/or homoplasy can be eliminated. Taxa H and I may be hybrids (Fig. 25). Nelson's method of examination of character conflict is only a beginning.

Microloma illustrates the use of the Nelson method to change the cladogram in Figure 26 (for characters for Figs. 26, 27 see Appendix J) to the one in Figure 27 by adding one reticulation and thereby shortening the cladogram.

Some groups have characteristics that cause difficulties when using Nelson's method. For instance, some have their origin in hybridization

but have since speciated (developed autapomorphies), some have numerous hybrids and even hybridization among hybrids, and some hybrids do not have all of the apomorphies of the parents (as in Fig. 2). The workability of Nelson's method is dependent on the hybrid inheriting the apomorphic characters from the parent taxa without too many character losses; otherwise the cladogram with the reticulations (Fig. 28; for characters for Figs. 28, 29 see Appendix K) will be longer than the most parsimonious cladogram without reticulations (Fig. 29). Also, this method is only feasible when the percentage of hybrids in the data set is low because the possibilities become endless, especially when the hybrids are hybridizing.

There are additional guidelines and methods that can be used when examining cladograms for possible hybrids. Use of these on seven data sets indicates that insights into the identification of possible hybrids and their parents can be gained by studying the character patterns of the cladograms as well as the distributions and ploidy levels of the taxa involved. Some of these guidelines and methods are elaborations and evaluations of previously published ideas and others are new.

GUIDELINES AND METHODS FOR IDENTIFYING
POSSIBLE HYBRIDS AND THEIR PARENTS

1. When there are two cladograms of similar length and one taxon position changes, the taxon that is moving may be a hybrid and the two taxa between which it is moving may be the parents. In Figures 3 and 4, taxon H (the hybrid) shifts between taxa A and B in the two most parsimonious cladograms. Taxon H may be a hybrid and A and B may be its parents. In Figures 15 and 16 taxon H shifts between taxa C and D and may be a hybrid.

2. As an extension of number 1, it is possible to follow a path of character conflicts. Figure 15 has characters 6 and 7 appearing twice and this identifies taxon D, the parent with which H (the hybrid) is not grouped. Figure 16 has 1, 3, and 5 appearing twice and this identifies taxon C, the parent with which H is not grouped. You do not have to have all of the characters. For instance, in Figure 16, H might not have character 3 (Fig. 30; for characters for Figs. 30, 31 see Appendix L) but as long as it had 1 and 5 taxon C would emerge as the other parent (Fig. 31).

3. Taxa that are defined solely by character conflicts may be hybrids or parents. In Figure
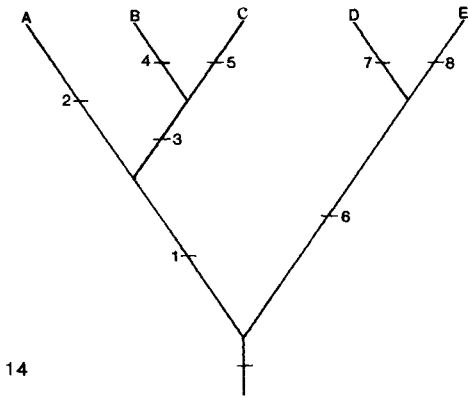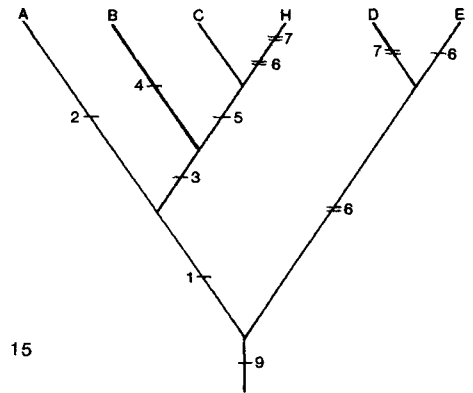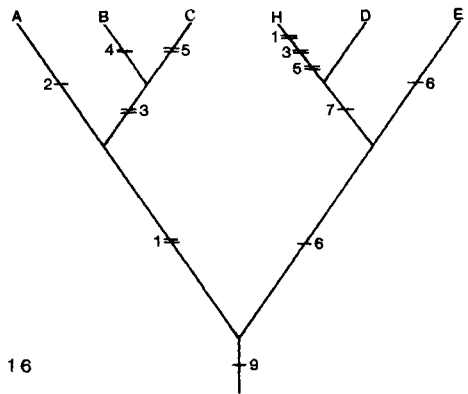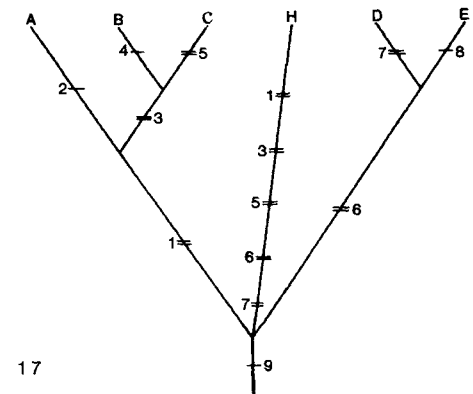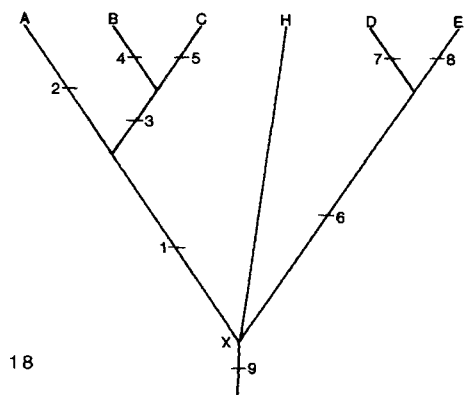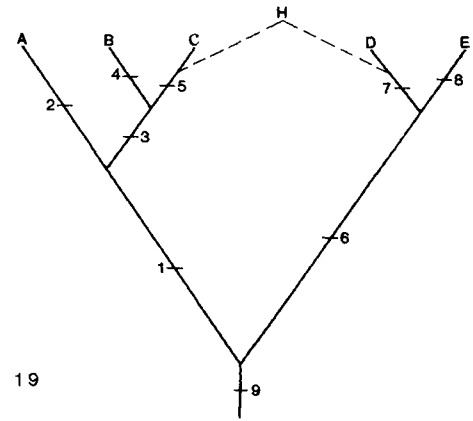
FIGURES 14–19.— 14–17, 19. Cladograms illustrating the pattern of species C and D and their hybrid, H.— 18. Cladogram illustrating when a polytomy is formed in the most parsimonious cladogram.

15, taxa H (the hybrid) and D are defined only by characters that appear elsewhere on the cladogram and in Figure 16, taxa C and H also have only homoplasies. The same is true for taxa C and B in Figure 20, taxa A and I in Figure 23, and taxa B and C in Figure 26.

4. Taxa with reversals may be hybrids. In Figure 32 (for characters for Figs. 32, 33 see Appendix M) taxon H (the hybrid) has not inherited all of the apomorphies of both parents and therefore is defined not only by characters that appear more than once on the cladogram but also by
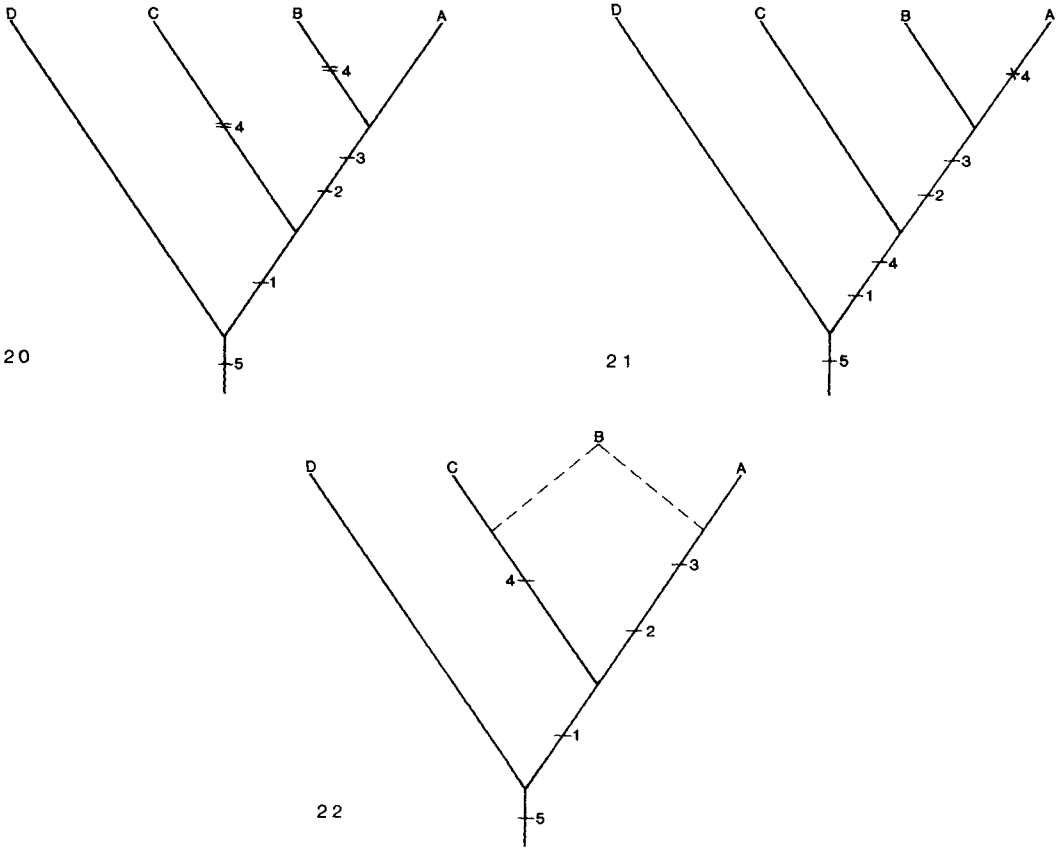
FIGURES 20–22.   Cladograms illustrating a simple example of the Nelson (1983) method for analyzing clado-grams for possible hybrids.
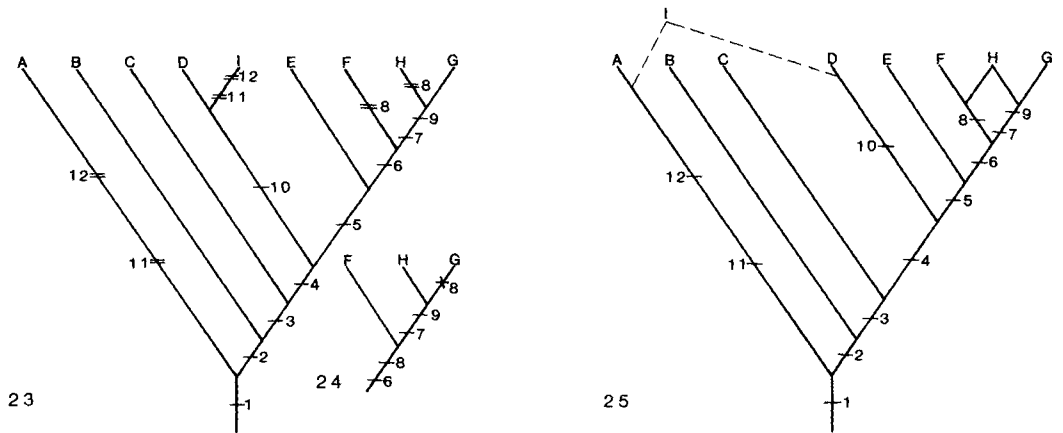
FIGURES 23–25.   Cladograms illustrating an example of the Nelson (1983) method for analyzing cladograms for possible hybrids.
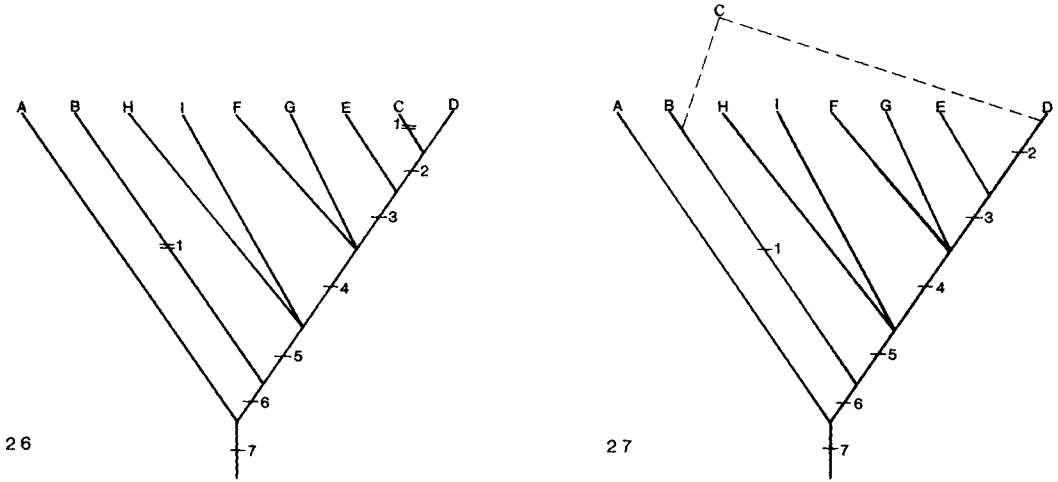
FIGURES 26, 27. Cladograms illustrating the use of Nelson's method for analyzing cladograms for possible hybrids in the genus *Microloma*.

character loss. Taxon H does not have characters 3 and 8 from taxon C and is also missing character 10 from taxon D. In fact, there has been enough inheritance of plesiomorphies to make the cladogram with reticulations (Fig. 33) the same length as the most parsimonious cladogram (Fig. 32). Another possibility is when there is one parent species rich in apomorphies and another lacking them altogether—hybrids might be intermediate or they might evidence multiple loss.

5. Taxa without autapomorphies may be parents. If the hybrid inherits all of the apomorphies of the parent with which it is grouped, then the parent will have no autapomorphies (Fig. 2, taxon A; Fig. 7, taxon A; Fig. 15, taxon C; Fig. 16, taxon D). If the hybrid fails to inherit any of the apomorphies of the parent with which it is not grouped, the hybrid will have no autapomorphies (Fig. 13, taxon H)—normally in evidence as homoplasies.

6. Consensus Trees—Consensus analysis is developing rapidly as an aid in evaluating a number of equally or nearly equally parsimonious cladograms. Consensus trees represent the information shared by two or more cladograms. The consensus tree is a compromise classifica-
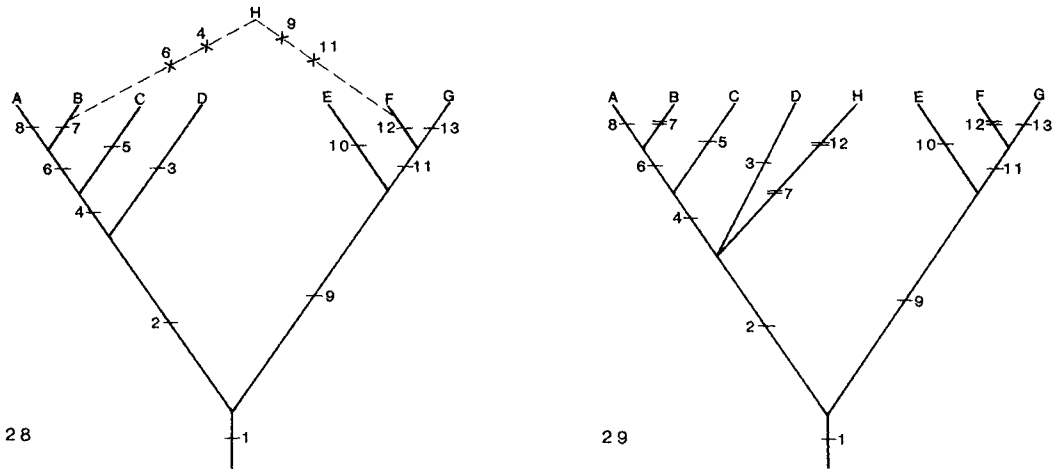
FIGURES 28, 29. Cladograms illustrating that the cladograms with reticulations are not necessarily the most parsimonious.
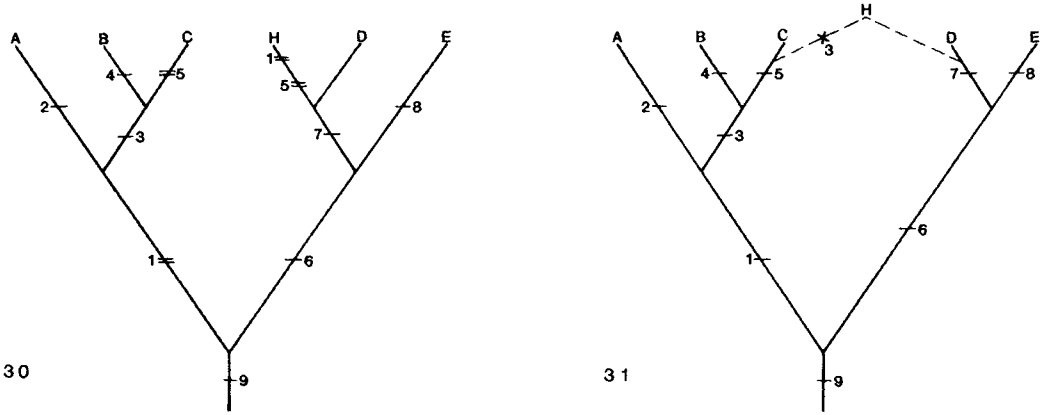
FIGURES 30, 31. Cladograms illustrating that possible parents can be identified even if all apomorphies of both parents are not present in the hybrid.

tion. Consensus trees were first developed by Adams (1972) and have been used in the context of comparing cladistic versus phenetic methods (Mickevich, 1978; Schuh & Polhemus, 1980; Sokal & Rohlf, 1981) or to compare a cladogram constructed from a chemical data set and an intuitive tree (Seaman & Funk, 1983). There are many different types of consensus analysis, Adams consensus (Adams, 1972), strict consensus (Sokal & Rohlf, 1981), majority consensus (Margush & McMorris, 1981), and *durchschnitt* consensus (Neuman, 1983). Only Adams consensus trees and Nelson component analysis will be discussed in this paper because of ease of use and explanation. For further investigation, other references include Mickevich (1978), McMorris et al. (1983), and a series of papers in Felsenstein (1983).

An Adams consensus tree (ACT) may have a topology different from any of the cladograms used to construct them. Figures 15 and 16 have a different topology, but if we concentrate on agreements we get Figure 14. Then we can add the taxon left out to the first node common to both of its positions (Fig. 17). A detailed discussion of how to construct an ACT is found in Adams (1972).

7. Component Analysis (NCA) was developed by Nelson (1979) as a consensus method. A component is any monophyletic group on a cladogram or phylogenetic tree. Every cladogram can be divided into a certain number of components that have more than one terminal taxon. In order to construct a Nelson Consensus Tree it is possible to add together components that are common to two or more cladograms. The
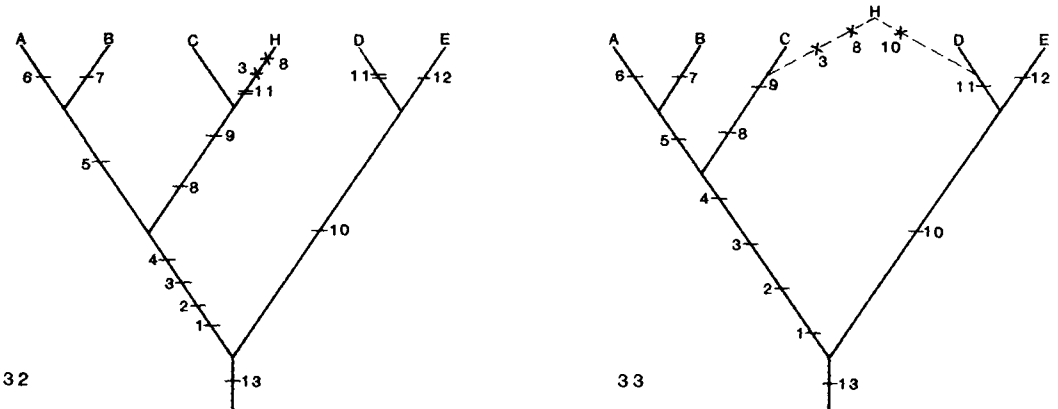
FIGURES 32, 33. Cladograms illustrating that character loss may be an indication of hybridization.
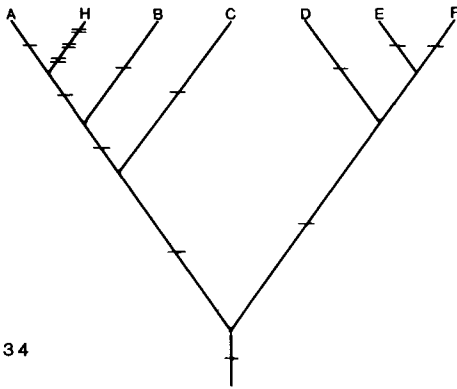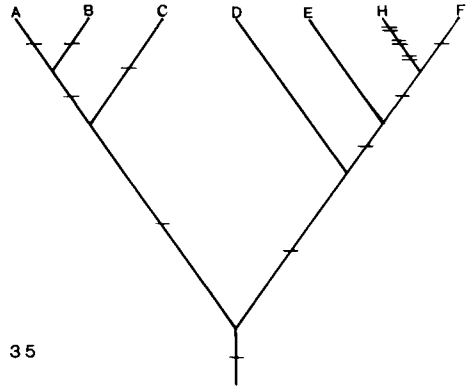
FIGURES 34, 35. Cladograms illustrating that by comparing the components (Table 1) one can identify the source of incompatibility.

movement of one taxon from one side of the cladogram to the other can have the effect of changing all of the components (Figs. 34, 35, Table 1) and no consensus tree can be constructed. However, instead of searching for complete agreement among the components, we can examine in what way they are different and identify which taxa are responsible for the lack of congruence. Examining the list of components for the two figures (Figs. 34, 35, Table 1) it is obvious that taxon H is causing the incompatibility.

These various suggestions are not to be used individually but collectively to generate hypotheses of hybridization. We can then turn to other forms of data to corroborate or falsify our hypotheses. Two of the most readily available in many groups are distribution and polyploidy, but others such as karyotyping and pollen fertility can be employed. We will see how such information can be used in the examples below. All cladograms were constructed manually.

EXAMPLE 1. *MICROLOMA* (ASCLEPIADACEAE)
BREMMER AND WANNTORP (1979)

Microloma is an African genus of 19 species, nine of which are represented in the most parsimonious cladogram (Fig. 36, Appendix J) and an alternative cladogram that is three steps longer (Fig. 37). Figure 37 shows taxon C sharing an apomorphy with taxon B and Figure 36 shows taxon C sharing four apomorphies with taxon D indicating that B and D may be the parents if C is a hybrid. Also, there is a path of parallel characters to follow to the parents especially in Figure 37. Furthermore, taxon D (Fig. 36) and taxon B (Fig. 37) have no autapomorphies, indicating they

might be the parents with which the hybrid is grouped. In addition, an ACT (Fig. 38) can be constructed that identifies the hybrid by placing it at the first node shared by the two parents. A NCA (Table 2) shows that C is responsible for the incompatibility between the two sets of components.

EXAMPLE 2. *ANACYCLUS* (ASTERACEAE)
HUMPHRIES (1979, 1981)

Anacyclus (Appendix N) is a genus of Mediterranean distribution with 14 species (Figs. 39–42). The monograph and subsequent paper by Humphries (1979, 1981) included a cladistic analysis and speculations on the hybrid origin for three of the species. Figure 39 is the most parsimonious cladogram (L = 45) for the data furnished by Humphries (1983); the number in parentheses next to the lower case letter indicates the number of apomorphies that have that pattern of distribution. If we concentrate on the character types that conflict with the most parsimonious cladogram (p, b, f, q, l) we can draw alternative cladograms that are slightly longer (Fig. 40, L = 50; Fig. 41, L = 52). Figure 40 has four character types in conflict (k, p, q, o) and a

TABLE 1. Components for Figures 34, 35.

Figure 34	Figure 35
AH	AB
AHB	ABC
AHBC	HF
EF	EHF
DEF	DEHF
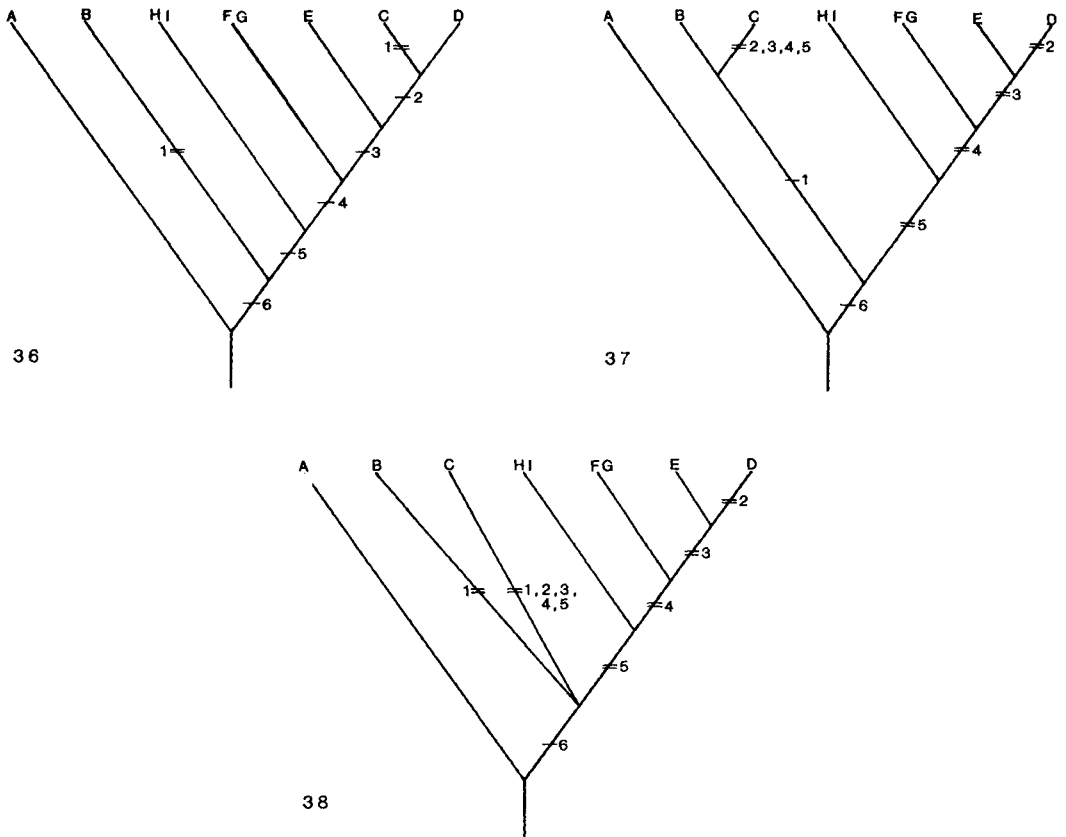
FIGURES 36–38.   Two cladograms of *Microloma* and their Adams consensus tree.

gain and subsequent loss of two character types (c, d). Figure 41 also has four types of conflict (o, b, c, q) and two types of loss (c, d). The consensus tree for these three cladograms is illustrated in Figure 42 and shows that four taxa are potential hybrids (N, C, I, J) because they have dropped in resolution and because they are defined either completely or primarily by characters that are found elsewhere on the cladogram. In addition by listing the components of the three figures (Table 3) it is evident that all of the com-

ponent incompatibility is caused by taxa I, J, C, and N. These four taxa are potential hybrids (Fig. 43) and their possible parents are as follows:

possible hybrids		possible parents
N	=	AB × EF-LM
I	=	G × H
J	=	G × H
C	=	AB × D-LM

Figure 43 is 42 steps long. Based on his analyses Humphries (1979, 1981) suggested three putative hybrids (N, I, J) and indicated corroboration for the hypothesis of hybridization for these three species. According to Humphries in addition to sharing apomorphies with AB and EF-LM, *A. officinarum* (N) is known only as an extinct cultivar grown in the nineteenth century for pharmaceutical reasons. *Anacyclus valentinus* (I) and *A. inconstans* (J) have florets of intermediate length between *A. clavatus* (G) and *A. homogamos* (H). Also, *A. valentinus* (I) is a weedy taxon

TABLE 2.   Components for Figures 36, 37.

Figure 36	Figure 37
CD	BC
ECD	ED
FGECD	FGED
HIFGECD	HIFGED
BHIFGECD	BCHIFGED
ABHIFGECD	ABCHIFGED
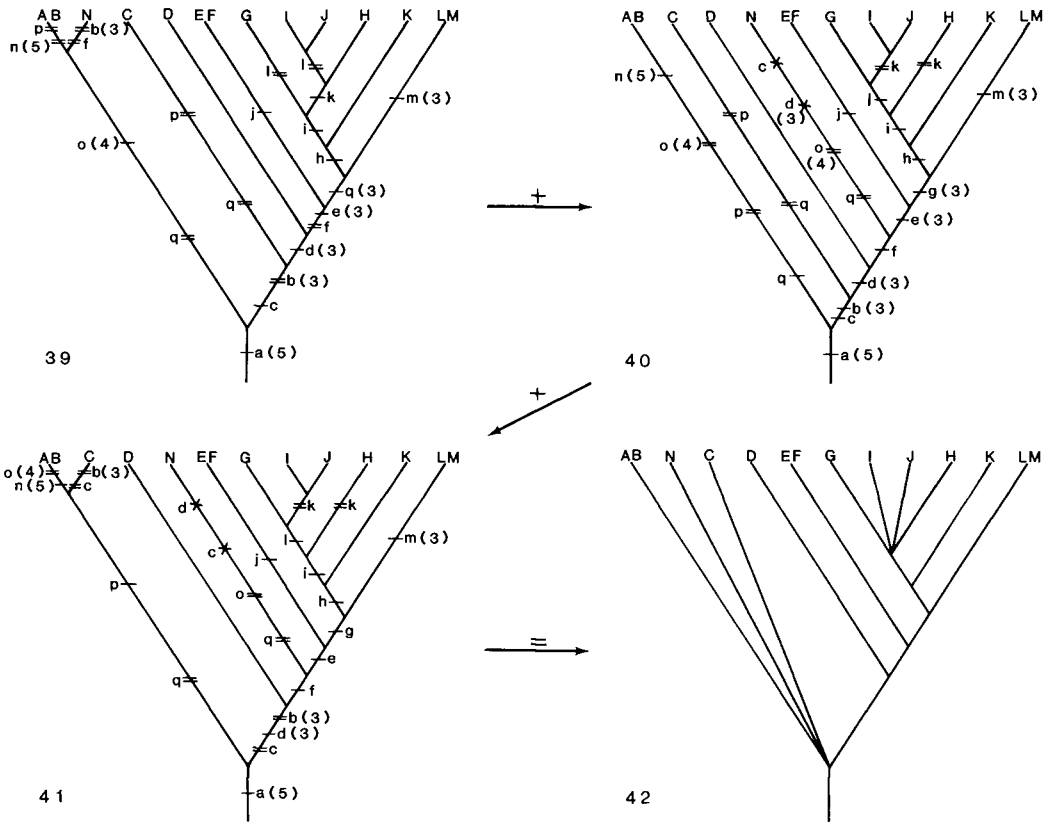
FIGURES 39–42. Cladograms of *Anacyclus*.

occurring only on disturbed land in the southwest Mediterranean region, and *A. inconstans* (J) occurs sympatrically with the Algerian population of *A. clavatus* (G). Cytogenetic studies carried out by Humphries (1981) corroborated the hypotheses of hybridity for *A. valentinus* (I) and *A. inconstans* (J). There was no material for cytogenetic studies available for either *A. officinarum* (N) or *A. monanthos* (C). There is, then, good reason to list both *A. valentinus* (I) and *A. inconstans* (J) as possible hybrids because the hypotheses of hybridity have been supported by independent data. *Anacyclus officinarum* (N) has been supported as a hybrid by its cultivated nature but is more difficult to analyze because it is not known to be extant. *Anacyclus monanthos* (C) was not indicated by Humphries to be of hybrid origin. In his monograph, Humphries

TABLE 3. Components for Figures 39–41.

Figure 39	Figure 40	Figure 41	Conflicts
IJ	IJ	IJ	
IJH	GIJ	GIJ	IJ
GIJH	GIJH	GIJH	IJ
GIJHK	GIJHK	GIJHK	
GIJHKLM	GIJHKLM	GIJHKLM	
EFGIJHKLM	EFGIJHKLM	EFGIJHKLM	
DEFGIJHKLM	NEFGIJHKLM	NEFGIJHKLM	N
CDEFGIJHKLM	DNEFGIJHKLM	DNEFGIJHKLM	C, N
ABN	CDNEFGIJHKLM	ABC	C, N
ABNCDEFGIJHKLM	ABCDNEFGIJHKLM	ABCDNEFGIJHKLM	
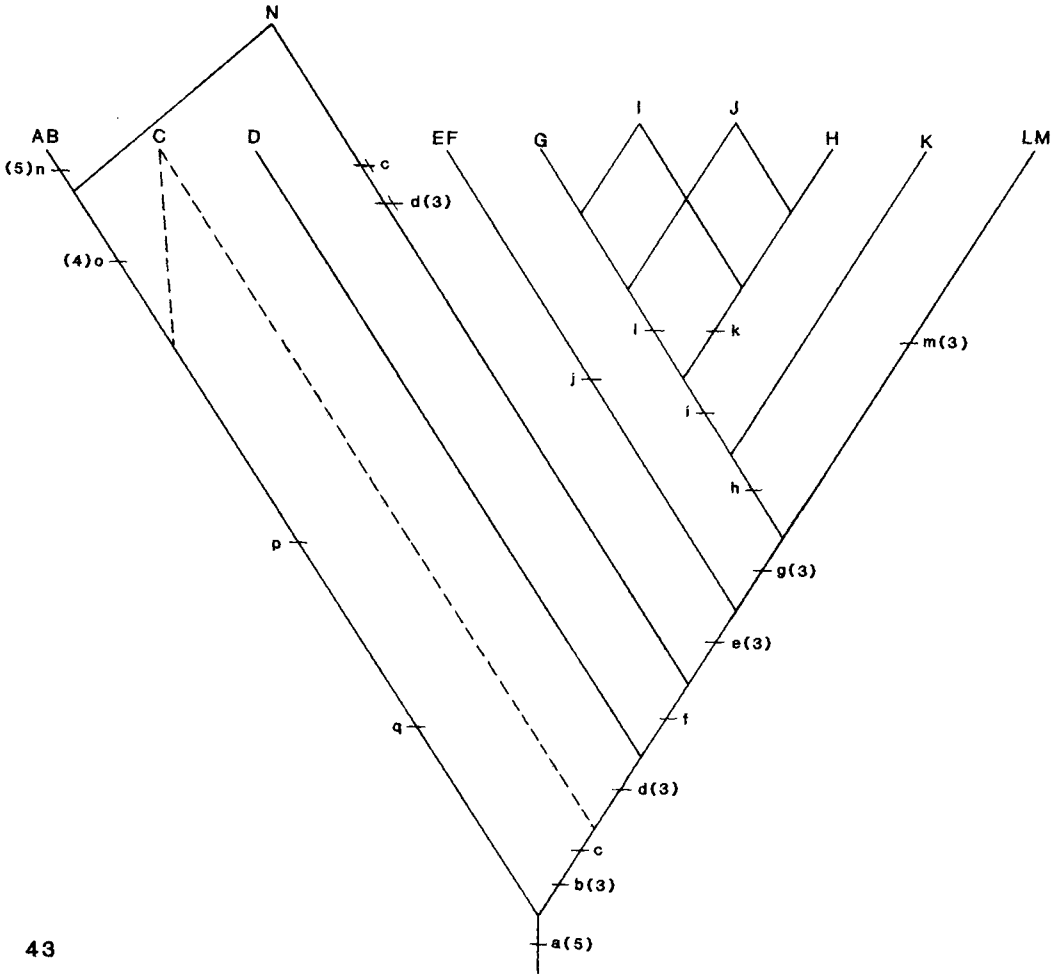
43

FIGURE 43.   Cladogram of *Anacyclus* with reticulations.

(1979) listed it as a pioneer of sandy soil and in some areas a dominant weed; these are characteristics of some hybrids. He also mentioned that it resembles one of the two subspecies of *A. homogamos* (H). However, Humphries thinks that *A. monanthos* (C) is a taxon exhibiting intermediate characters and not a hybrid because it has many autapomorphies (Humphries, pers. comm.). Because of the lack of additional information on this taxon I have left it as a dotted line on the cladogram (Fig. 43).

The cladogram in Figure 43 differs from that of Humphries because I emphasized reducing the number of parallel characters and was not as concerned if this created additional character losses. Therefore, taxon N is connected as an internode further along the diagram. This is important because it is, in my opinion, unlikely that

a hybrid will inherit all of the apomorphies of both parents. Thus, some plesiomorphies will be inherited resulting in the loss of some characters. The apomorphies that are inherited are the guide to the identification of possible parents.

Anacyclus is a good example of the use of cladistics to identify possible hybrids and then employing other techniques including karyotyping and chemical analysis, distribution, and habitats to further corroborate or falsify the hypotheses of hybridization (Humphries, 1979, 1981).

EXAMPLE 3. *AGASTACHE* (LAMIACEAE)
SANDERS (1982, AND IN PREP.)

The 14 species of *Agastache* Clayt. sect. *Brittonastrum* (Appendix O) are all diploid and are confined to the cordilleras of the southwest United
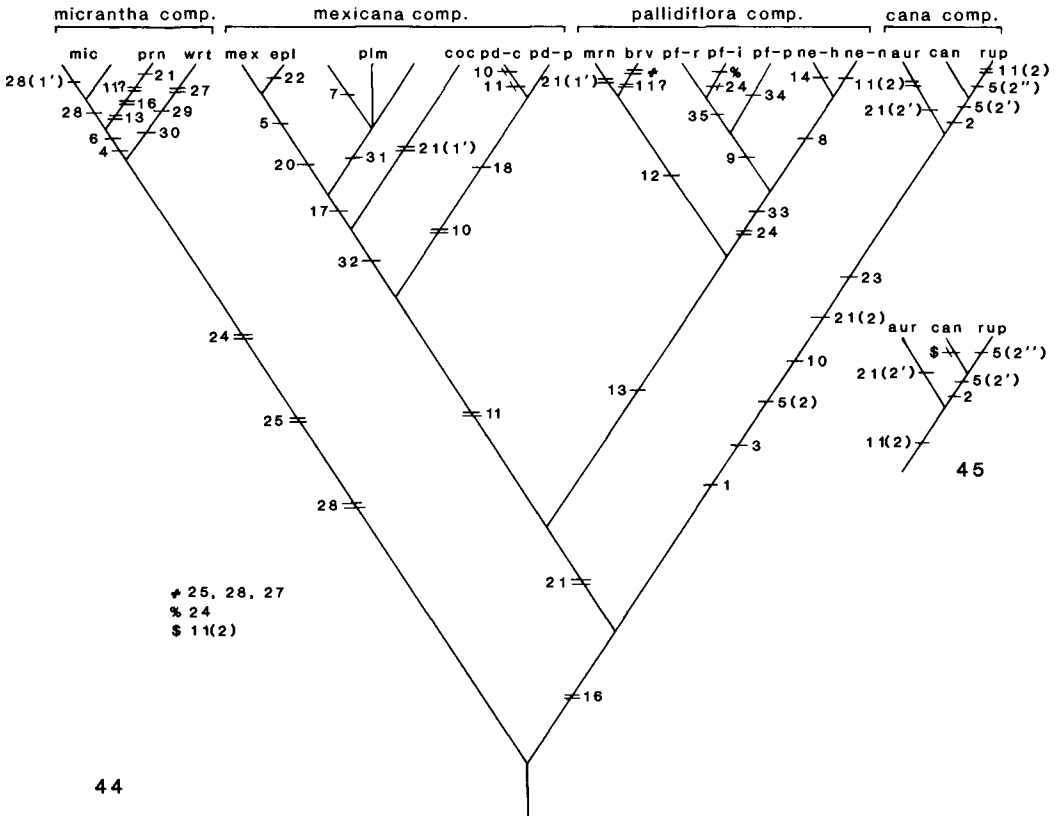
FIGURES 44, 45. Cladograms of *Agastache*.

States and Northwest Mexico. Looking at the parsimony cladogram (Figs. 44, 45) there are taxa with no autapomorphies (*A. pallidiflora* var. *neomexicana* ne-n, *A. pallidiflora* var. *greenei* pf-r, *A. mexicana* mex), taxa with only character conflicts (*A. breviflora* brv, *A. mearnsii* mrn, *A. coccinea* coc, *A. pringlei* prn), and taxa with character losses (*A. pallida* var. *coriacea* pd-c, *A. pallidiflora* var. *gilensis* pf-i). Three of these taxa (prn, brv, pd-c) are immediately identifiable as possible hybrids, *A. pringlei* and *A. breviflora* because they have four character conflicts each and *A. pallida* var. *coriacea* because it has two character losses. Less strongly indicated are *A. pallidiflora* var. *gilensis* (because of the absence of character 24 and some connection with *A. coccinea*) and *A. mearnsii* [because of character 21(1′)]. Examining each one individually, *A. breviflora* has characters 25, 26, and 27 (and sometimes 11). If *A. breviflora* is a hybrid then one parent (*A. mearnsii*) could be its sister species. In order to identify a candidate for the second parent, emphasize the characters *A. breviflora* has

and not the characters it does not have. Then locate where else on the cladogram these characters are found (25, 26, and 27; Fig. 44). The presence of these three characters indicates *A. wrightii* (wrt) as the other possible parent. Comparing the geographical distributions (Sanders, pers. comm.), *A. breviflora* and *A. wrightii* are sympatric in southern Arizona, southwest New Mexico, and northern Sonora and Chihuahua. *Agastache mearnsii* is found a short distance from *A. wrightii* in southern Sonora and Chihuahua. The distribution pattern would suggest a hybridization event is possible.

A second possible hybrid, *A. pringlei* (prn) is sister to *A. micrantha* (one subspecies of which has no autapomorphies). *Agastache micrantha* has four character conflicts (13, 16, 21, and sometimes 11, see Appendix O). Locating the apomorphies on the cladogram identifies the "Pallidiflora complex," which contains *A. breviflora, A. mearnsii,* and the five subspecific taxa of *A. pallidiflora. Agastache pringlei* is sometimes sympatric with *A. micrantha* (southern

micrantha comp. mexicana comp. brv pallidiflora comp. cana comp.

coc

prn

mic wrt mex epl plm pdp pdc mrn pf-r pfp ne-h ne-n aur can rup

pf-i
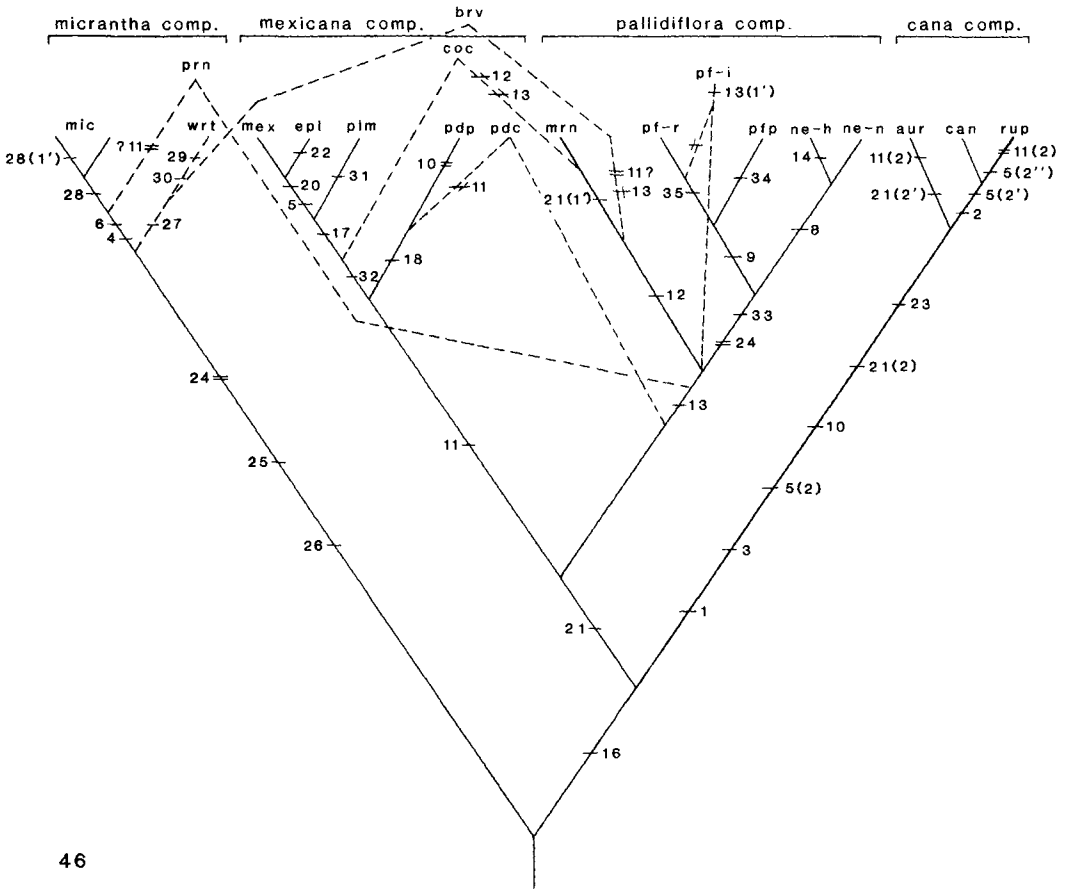
FIGURE 46. Cladogram of *Agastache* with reticulations.

Chihuahua and southern New Mexico) and parapatric with *A. mearnsii* (southern Chihuahua and the Chihuahua/Sonora border). The *A. pallidiflora* subspecific taxa and *A. breviflora* are distributed in the southwest United States. If *A. pringlei* is a hybrid the most likely putative parents are *A. micrantha* and *A. mearnsii*.

A third potential hybrid, *A. pallida* var. *coriacea* (pd-c), is sister to *A. pallida* var. *pallida* and has two character losses. If *A. pallida* var. *coriacea* is a hybrid and one parent is *A. pallida* var. *pallida* then the other parent is probably something that lacks characters 10 and 11; possibly something in the "Pallidiflora complex" because the putative hybrid has characters 16 and 21. Based on geographical distribution, the most likely parent in the "Pallidiflora complex" is *A. mearnsii* that has a parapatric distribution with *A. pallida* var. *coriacea*.

The last two possible hybrids, *A. coccinea* (coc)

and *A. pallidiflora* var. *gilensis* (pf-i), are more difficult to place because they have less information (fewer characters). We can estimate that *A. coccinea* is a hybrid and that one parent may be found in the group defined by character 32; because of the presence of character 21(1') the other parent would probably be *A. mearnsii*. The distribution of the species does not help in this case because several of the taxa are sympatric.

The final taxon considered as a hybrid is *A. pallidiflora* var. *gilensis*. This taxon might be the result of a cross between *A. pallidiflora* var. *greenii* and some taxon without character 24. All taxa in the "Pallidiflora complex" that have a distribution that would allow for the formation of this hybrid have character 24 except *A. mearnsii*. However, *A. pallidiflora* var. *gilensis* has an autapomorphy, and this makes it less likely that it is of hybrid origin (but does not exclude it). Based on this analysis the following hybrids are pos-
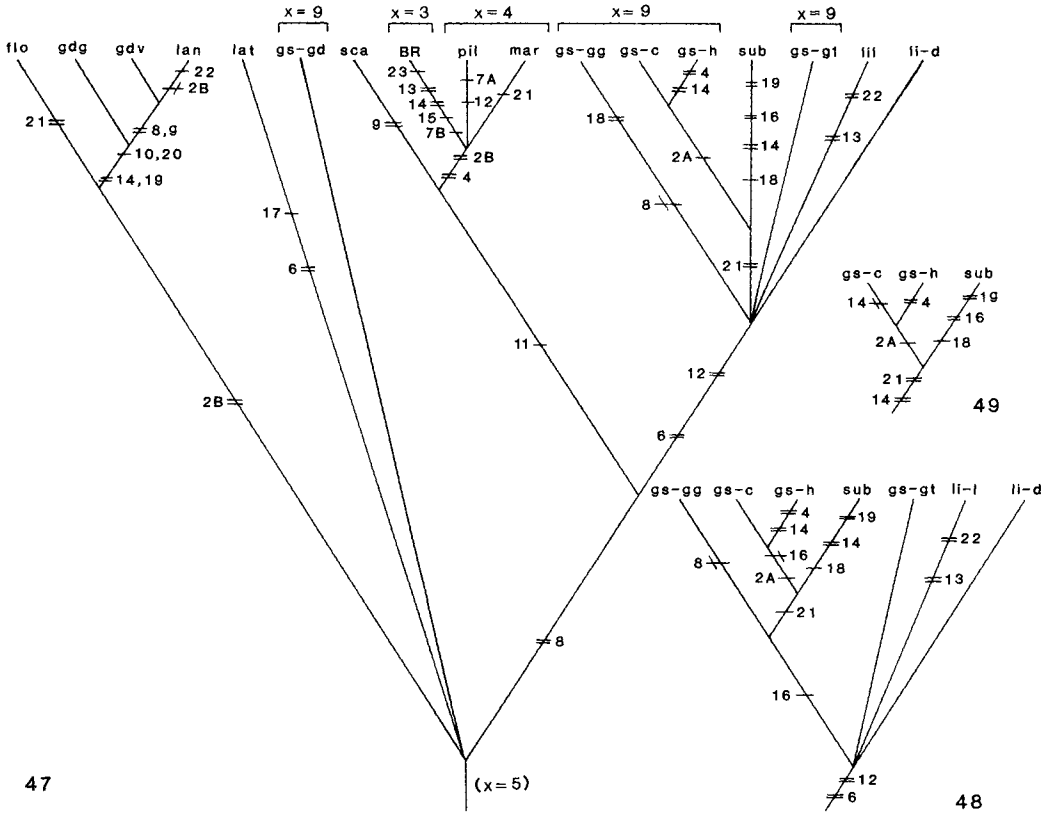
FIGURES 47–49.   Cladograms of *Chrysopsis* and *Bradburia*.

sible: brv = wrt × mrn, prn = mic × "Pallidiflora complex," pd-c = pd-d × mrn, coc = mrn × mex-plm, and pf-i = pf-r × some taxon without 24 (possibly mrn).

Figure 46 shows the hypothesized hybrids and their possible parents. According to Sanders (1981), the hybrids and their parents are as follows: brv = wrt × mrn, prn = mic × mrn, pd-c = pd-p × mrn, coc = pfr × mrn (mex-epl + mrn), and pf-i = pf-r × mrn (pf-f − pf-r + mrn). Although Sanders' estimates are in some cases more specific, there are no conflicts.

EXAMPLE 4. *CHRYSOPSIS* AND *BRADBURIA* (ASTERACEAE) SEMPLE (1981, AND PERS. COMM.), SEMPLE AND CHINNAPPA (1984)

Chrysopsis (Nutt.) Elliot (Appendix P; 10 species) and *Bradburia* Semple & Chinnappa (Appendix P; 1 species) are yellow-rayed golden-asters distributed in the southeast United States (especially Florida) except for one species of *Chrysopsis* that occurs in the eastern United

States. Using the characters furnished by Semple three cladograms were constructed (Figs. 47–49). There is a high level of homoplasy in the clado-gram because only nine apomorphies lacked character conflicts and only four of these 11 are synapomorphies (10, 20, 11, 2A). Such a high level of character conflict and character loss is an indication of possible hybridization. The chromosome numbers were not used as char-acters in the analysis and are indicated on the cladogram to facilitate the discussion. Also, there is one report of $x = 4$ for *Bradburia* that is not indicated on the cladogram.

Taxa *C. lanuginosa* (lan), *C. gossypina* subsp. *gossypina* f. *gossypina* (gs-gg), *C. gossypina* subsp. *hyssopifolia* (gs-h), and *C. linearifolia* subsp. *li-nearifolia* (li-l) are defined only by character con-flicts and/or character losses and may be hybrids themselves or the parent with which another hy-brid is not grouped. Two taxa *C. godfreyi* f. *viri-dis* (gd-v) and *C. gossypina* subsp. *cruiseana* (gs-c) are possible parents with which the hybrids are grouped because they have no autapomorphies
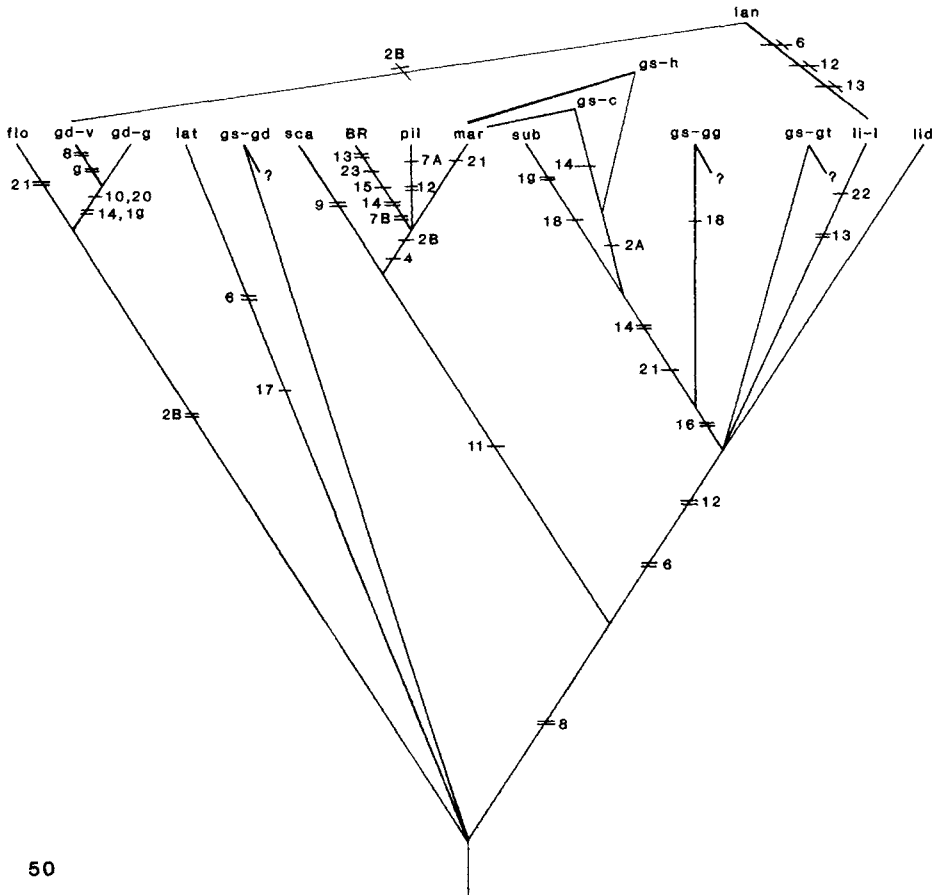
FIGURE 50. Cladogram of *Chrysopsis* and *Bradburia* with reticulations.

and have a single taxon as a sister taxa. If we construct hypotheses based on these data we obtain the following results: lan = gd-g × li-l, gs-c & h = sub × pil or mar, and gs-gg = sub × some taxon without 8. Because so many of the taxa are sympatric or parapatric, the distributions are not of much assistance in refining the hypotheses. The exceptions are *C. gossypina* subspp. *cruiseana* and *hyssopifolia* (gs-c & h) that can be attributed to a cross between *C. subulata* and *C. mariana* (sub × mar).

There are four taxa with no autapomorphies [gd-g (*C. godfreyi* f. *godfreyi*), gs-gd (*C. gossypina* subsp. *gossypina* f. *decumbens*), gs-gt, li-d)] that are potential hybrids or parents. Their chromosome numbers show that all of the gs taxa are $x = 9$, and based on outgroup comparison the base number for the genera is probably $x = 5$ (this agrees with Semple, 1981). Therefore, the subspecific taxa of *C. gossypina* are most likely

hybrids. This supports the hypotheses of hybridization for three of the subspecific taxa of *C. gossypina* (gs-gg, gs-c & h), however *C. gossypina* f. *trichophylla* and f. *decumbens* (gs-gt, gs-gd) were not identified, except for noting that they lacked autapomorphies. The cladogram clearly indicates why *C. gossypina* f. *decumbens* was overlooked, it has no synapomorphies or autapomorphies. If it is a hybrid it is an excellent example of a hybrid inheriting all plesiomorphies of both parents and appearing in an ancestral position on the cladogram. Likewise, *C. gossypina* f. *trichophylla* was overlooked because it inherited most, but not all, of the plesiomorphies. The chromosome number of $x = 5$ does not support, and in fact falsifies, the hypothesis of hybridization for *C. lanuginosa* because one of the hypothesized parents has $x = 5$ and the other $x = 9$.

Figures 47–49 show that the $x = 9$ taxa do not
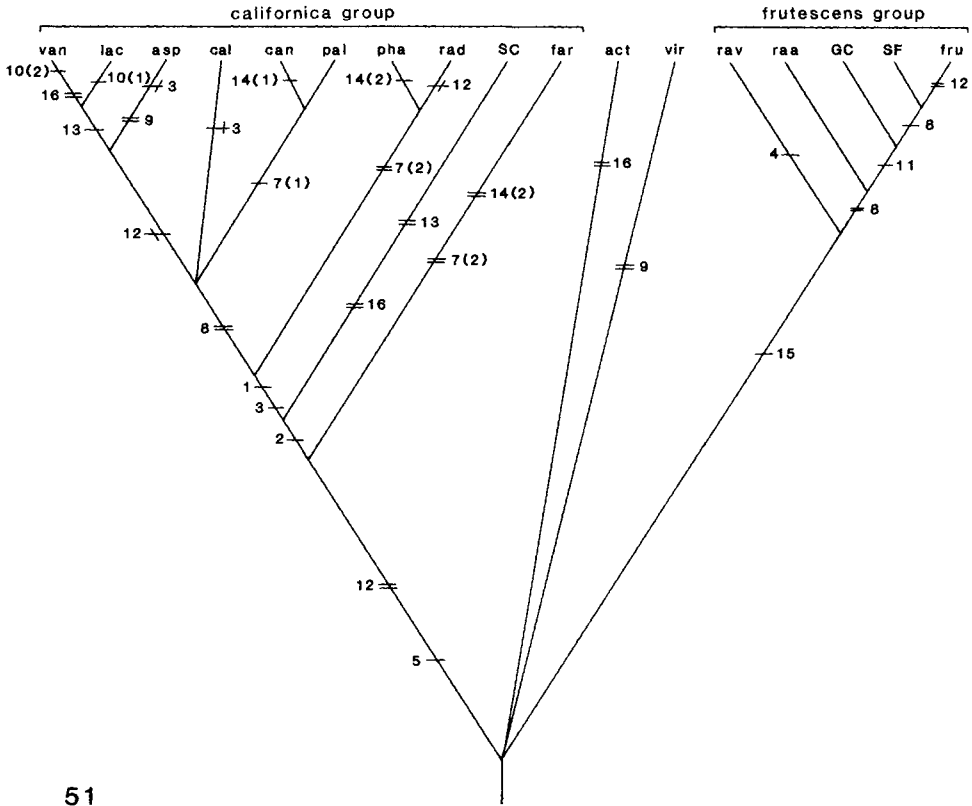
FIGURE 51. Cladogram of *Encelia*.

form a monophyletic group. Semple (1981) proposed that the $x = 9$ group is from one hybridization event between an individual of *C. subulata* and one of *C. mariana* with subsequent selections to give different combinations of parental genes. The cladogram does not support that statement because of the different combinations of characters in the five different subspecific taxa. However, it also does not reject Semple's suggestion. It simply suggests that one should also consider the possibility of several different hybridization events involving the same species as parents with different characters being inherited each time (Fig. 50).

Using cladistics alone has not given us a clear answer to the question of hybridization in *Chrysopsis* and *Bradburia*, however when the hypotheses of hybridization are tested with additional information, such as distribution and ploidy level, we have been able to make five putative hybrids and gain some insight into possible parents.

EXAMPLE 5. *ENCELIA* (ASTERACEAE)
(CLARK, PERS. COMM.)

Encelia Adanson (Appendix Q) comprises 18 taxa distributed in the western United States. All taxa are diploids. The data matrix and the taxon distributions were furnished by Curtis Clark.

There are at least two cladograms that are equally parsimonious (Figs. 51, 52) and one that is one step longer (Fig. 53); all have different branching patterns. There are several additional cladograms that have slightly different character distributions but do not have different branching patterns, and these are not illustrated. On the three cladograms there are several taxa that change positions. *Encelia farinosa* can be placed as the sister taxa of *E. farinosa* var. *phenicodonta* (Figs. 52, 53) or near the base of the cladogram (Fig. 51). In either case it is only defined by character loss and/or homoplasy. Likewise *E. asperifolia* is either the sister taxon of *E. ventorum/E. laciniata* (Fig. 51) or it is near the basal node (Figs. 52, 53). In all three positions *E. asperifolia*

californica group   frutescens group

ven lac rad far phe can pal asp cal SC act vir rav res GC SF fru
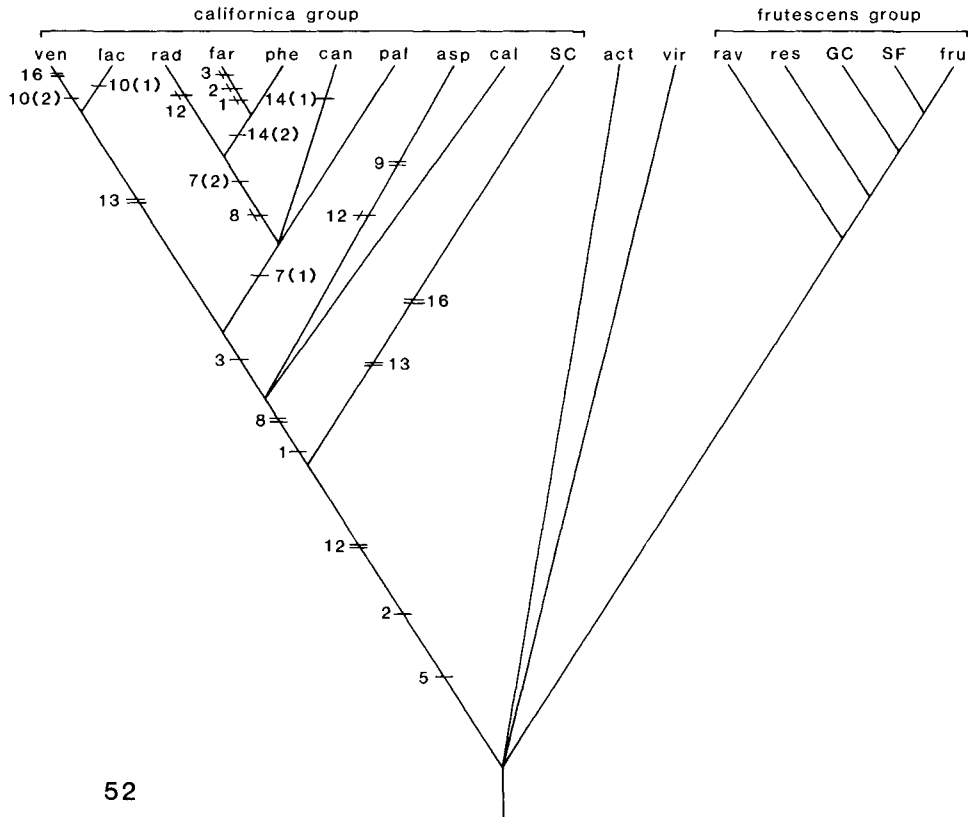
FIGURE 52. Cladogram of Encelia.

is identified by character loss and/or homoplasy. *Encelia canescens* is either the sister taxon of *E. palmeri* (Fig. 51) or it shares the node defined by character 7(1) with several other taxa (Figs. 52, 53). Two other taxa have some indication that they may be hybrids, *E. laciniata* with intermediate character 10(1) and the unidentified taxon from Santa Carla (SC) that is always defined by character homoplasy. There are three taxa that can be indicated as possibilities but cannot be placed as hybrids, ancestors, or parents because they have few apomorphies. Two taxa (*E. virginensis* and *E. actoni*) have only one apomorphy each and they appear on the cladogram at the basal node, and *E. californica* has a slight change in position depending on whether character 3 is treated as a character loss or not (Figs. 51–53).

Encelia farinosa and *E. asperifolia* stand out because of character losses and homoplasy. The best estimate for *E. farinosa* is that it is a hybrid between *E. farinosa* var. *phenicodonta* (its sister taxon in Figs. 52, 53) and something without characters 1, 2, and 3. *Encelia asperifolia* may be a hybrid between something without characters 3 and 12 (perhaps something in the "Frutescens group") and something in the "Californica group" with character 8 (perhaps *E. californica* with which it is closely grouped and whose lack of apomorphies may account for *E. asperifolia*'s similar situation). *Encelia canescens* might be a hybrid, between *E. palmeri* its sister taxon in Figure 51 and *E. farinosa* var. *phenicodonta*, because of the intermediate nature of character 14. *Encelia laciniata* may be a hybrid between *E. ventorum* and some other taxon that has not left a trace. If so, *E. laciniata* is an example of a hybrid inheriting all of the apomorphies of one parent. If the taxon from Santa Clara (SC) is a hybrid, one parent might be *E. ventorum* because of characters 13 and 16 and the other parent something from the "Californica group" that has character 12. A summation of possible hybrids is as follows: far = phe × some-
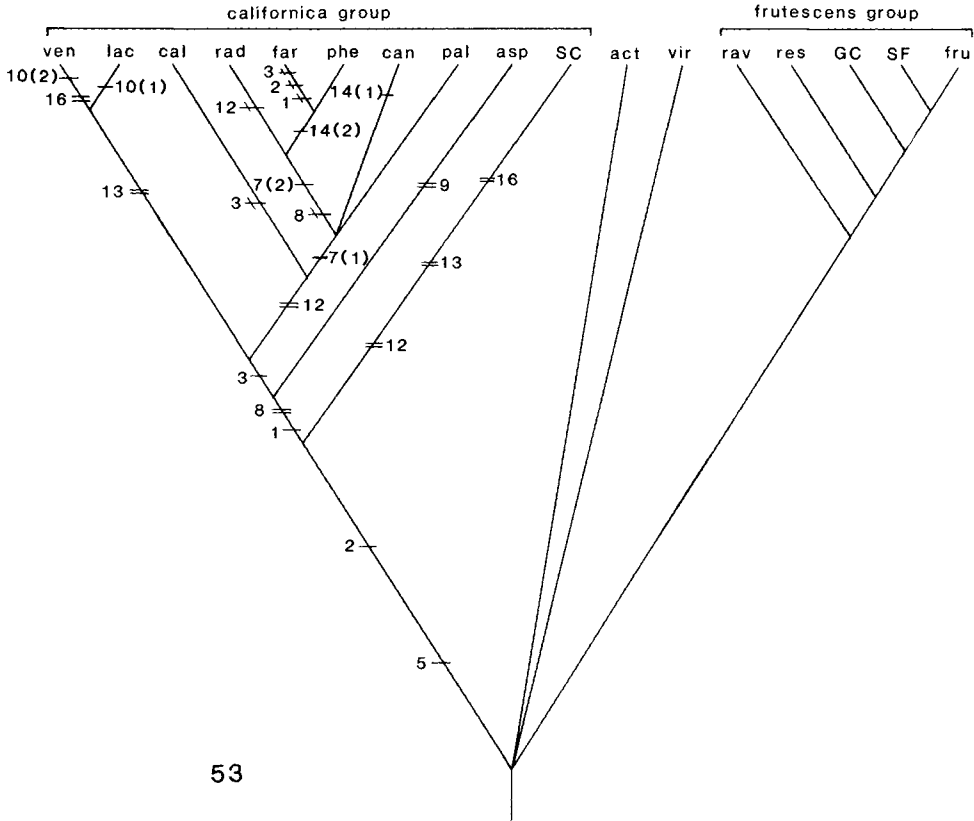
FIGURE 53.   Cladogram of *Encelia*.

thing without 1, 2, and 3, asp = cal × something in the "Frutescens group" with 8, can = pal × phe, lac = ven × ?, and SC = ven × "Frutescens group" with 12.

Listed above are five hypotheses of hybridization and some possible parents. Examination of the distribution patterns and other data do not support two of the hypotheses (*E. farinosa* and SC) and an additional one is added. An F_1 that has been identified as *E. virginensis* has been found growing with *E. actoni* so that *E. virginensis* should be investigated as a possible hybrid with *E. actoni* as one of the parents.

Using the distributions we can narrow down the choice of possible parents to the following: asp = cal × SF, can = phe × pal, lac = ven × ?, and vir = act × ?.

The reticulate cladogram is illustrated in Figure 54. The hybrids indicated with solid lines are those that were supported as hybrids by both the cladistic analysis and the distributional data; those with dotted lines were supported by only one of the two.

EXAMPLE 6.   *MONTANOA* (ASTERACEAE)
(FUNK, 1982)

Montanoa Cerv. (Appendix R) has 20 species in Mexico and Central America and five in northern South America. Examining one of the equally parsimonious cladograms (Fig. 55), only one taxon (*M. hexagona*) shows any strong indication of hybridization. This taxon has the only two character losses on the cladogram. There are however, three known high level polyploids in the genus (Fig. 55). Two of these (*M. revealii* and *M. guatemalensis*) show no evidence of being hybrids. The third is *M. hexagona* and, it could be a hybrid between its sister taxon, *M. hibiscifolia*, and something outside of the group defined by character 34. None of the polyploids are sympatric with any other species and they all have at least 95% pollen viability, and during meiosis there is at least one stage where a complete bivalent can be observed. So, we are left with these three species being either very old polyploids, two of which have developed autapo-
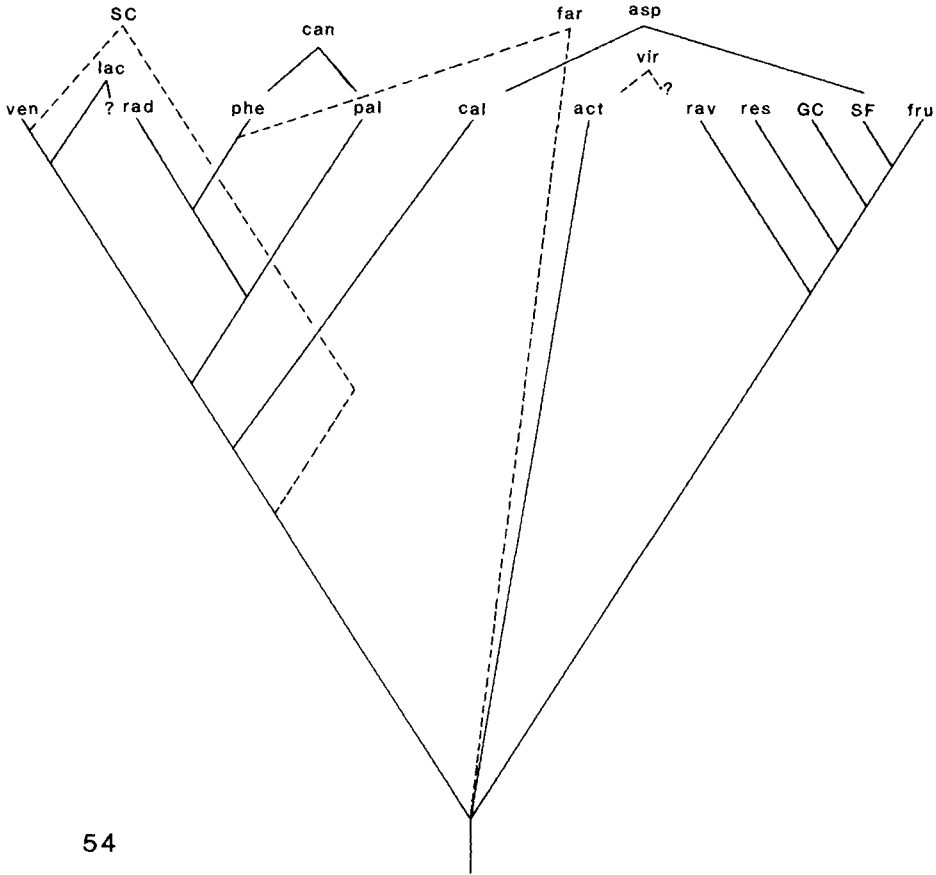
FIGURE 54. Cladogram of *Encelia* with reticulations.

morphies, or the parents are extinct so the relationships do not show up on the diagram. Or, less likely, they are autopolyploids with the diploids no longer extant. The cladogram cannot help us in resolving this matter.

EXAMPLE 7. *ACMELLA* (ASTERACEAE)
(JANSEN, IN PRESS)

This last example presents the most difficult case: one where there are more hybrids than non-hybrids in a genus, where the hybrids are hybridizing, where there are few characters in the analysis and some of the hybrids have inherited mostly plesiomorphies, and where the hybrids are weeds that disperse readily and tend to hybridize wherever they are. Although not the rule, such situations are not that unusual in the Asteraceae family. One such genus is *Acmella* (Appendix S). The species of *Acmella* used to be part

of *Spilanthes* Jacq. but were removed by Jansen (1981). There are 39 taxa (30 species), 16 of which are diploids (23 polyploids; ploidy level is estimated in some species, see Appendix S). The genus is pantropical with one species in the southeast United States. Some species form autopolyploid series that would allow them to cross with allopolyploids. Also, some reproduce asexually so odd level polyploids persist in nature.

There are at least ten equally parsimonious cladograms of *Acmella* and a large number (over 100) that are only a few steps longer. Many of these cladograms have very different structures. I have selected one to discuss as a representative (Fig. 56), but in no way am I indicating that this particular cladogram is to be preferred over any other. In Figure 56 there are only three apomorphies (excluding autapomorphies) that are not either subsequently lost or found elsewhere on the cladogram [7, 1, 2(2)]. The three major
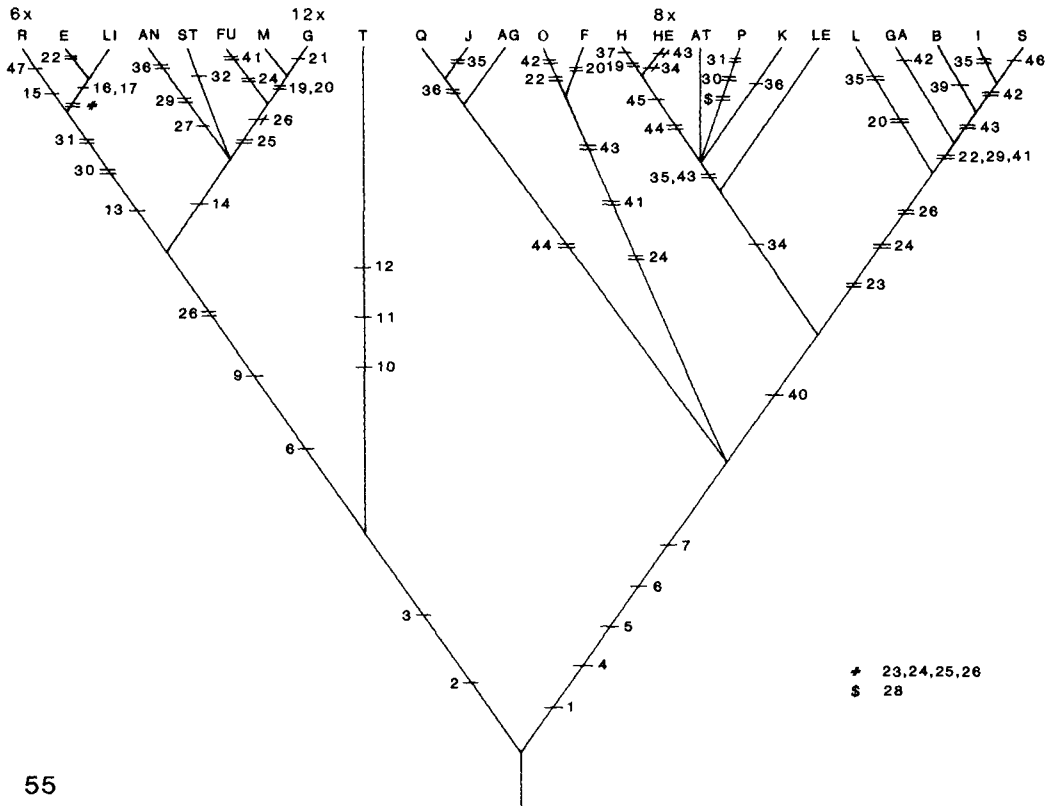
FIGURE 55. Cladogram of *Montanoa*, numbers above taxa indicate ploidy level of known polyploids.

groups of Jansen (in press; indicated in Fig. 56 by the large numbers 1, 2, and 3) are obvious on the cladogram and only one, number 2, is non-monophyletic (this group was non-monophyletic on all of the cladograms that I constructed). Some taxa may be hybrids between the three major groups, some of the more obvious ones are as follows:

1. *A. decumbens* var. *decumbens* (23a) may be a hybrid between some taxon in group 1 and one in group 2 because it has apomorphies 1 and 2.

2. *A. poliolepidica* (1) may be a hybrid between a taxon in group 1 that has apomorphy 20 and a taxon in group 3 with apomorphy 16.

3. The ancestor of *A. darwinii* (7) and *A. sodiroi* (8) may have been a hybrid between a taxon in group 2 and one in group 3 that has apomorphies 18(2) and 17(2).

4. *A. paniculata* (19) may be the hybrid of a taxon in group 3 and one outside of it because of its lack of apomorphy 22 (only two taxa in group 3 lack apomorphy 22).

Other taxa show some indication of hybridization within the groups. However, there is no strong indication of hybrids and their parents within the groups because there are so many alternative groupings and so few characters. Some taxa are obviously hybrids or of hybrid ancestry because of their ploidy level (Fig. 56, Appendix S) but there is little indication of what their history might be. The different parsimony cladograms give us different possible hybrids and parents. With the exception of two or three small groups of species that appear repeatedly on many, if not all, of the cladograms there are a few additional questions, such as biogeography, character evolution, or ecology that can be investigated using these cladograms. To a large extent we are dealing with straight character patterns.

We have apparently reached the limits of cladistics with genera such as *Acmella*. I say this because cladistics is merely an organized way of looking at the relevant data that have been gathered. If no consistent pattern develops using cladistics then the data are responsible, not the
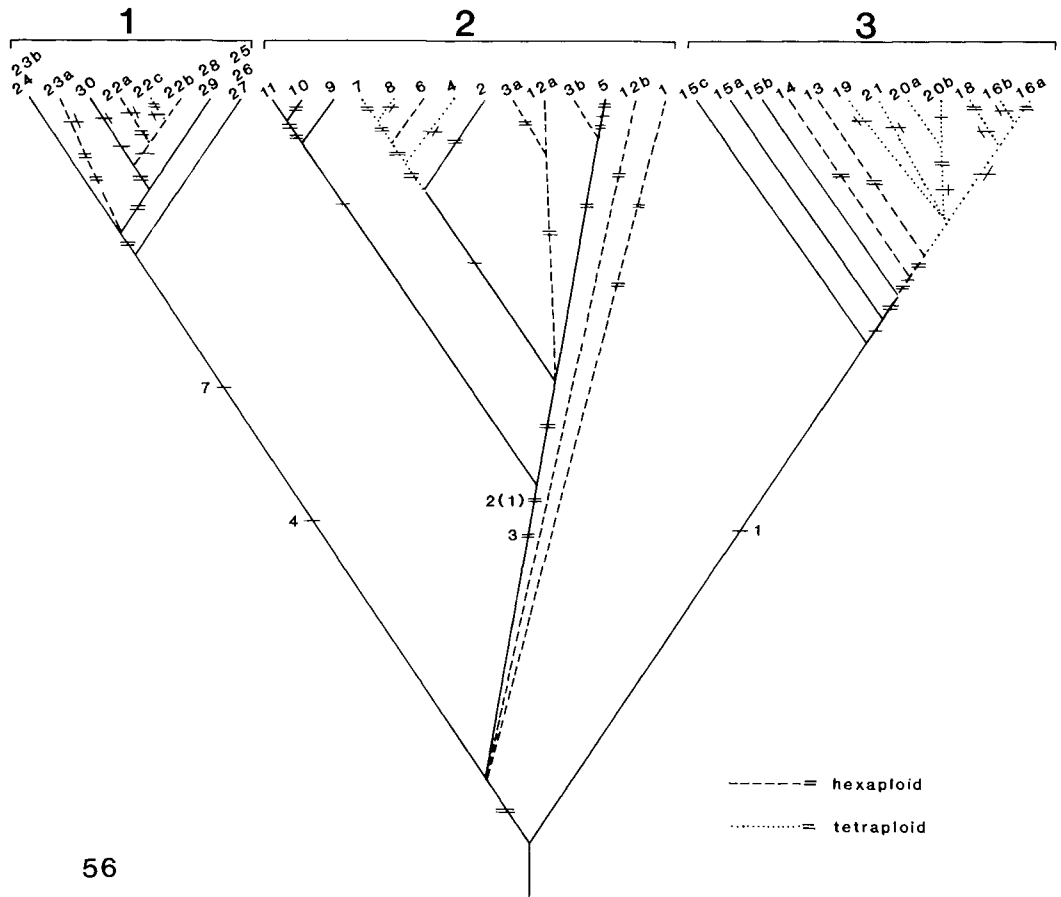
FIGURE 56.   One of the many equally parsimonious cladograms for *Acmella,* many of which have different topologies.

method. So the lack of resolution in genera such as *Acmella* is simply a reflection of the data. In the future we may be able to gain more information from genetic level research to increase the data base and obtain further resolution from cladistic analyses.

CLASSIFICATION OF HYBRIDS

A number of papers have been published that discuss the possibilities of classifying hybrids (Wiley, 1979; Wagner, 1980; Humphries, 1983; Humphries & Funk, 1984; Nelson, 1973) so the alternatives need not be discussed in this paper. As discussed in Humphries and Funk (1984), I prefer the method called phyletic sequencing or the annotated Linnean Hierarchy. This method works on the basic principle that all information from a cladogram is available in a classification

and that a cladogram can be reconstituted from a classification. In such a classification only monophyletic groups are recognized. An example using the genus *Anacyclus* from Figure 39 is listed below:

Classification of *Anacyclus* without hybrids
    Anacyclus
        A. pyrethrum
        A. monanthos
        A. maroccanus
        A. radiatus
        Clavatus species group
            A. linearilobus
            A. clavatus
            A. homogamos
        A. latealatus
        A. nigellifolius

The hybrids can be added in several ways; one

is to make them the sister taxon of either one of the parents. Using the first parent in the phyletic sequence we arrive at the following classification:

Classification of *Anacyclus* with hybrids
 Anacyclus
  Sect. *Pyrethraria*
   A. pyrethrum
   +*A. officinarum* sedis mutabilis (*A. pyrethrum* × *radiatus*)
  Sect. *Anacyclus*
   A. monanthos
   A. maroccanus
   A. radiatus
   Clavatus species group
    A. linearilobus
    A. homogamos
    +*A. inconstans* sedis mutabilis (*A. homogamos* × *clavatus*)
    +*A. valentinus* sedis mutabilis (*A. monogamos* × *clavatus*)
    A. clavatus
    A. latealatus
    A. nigellifolius

The special notations include a plus sign (+) for hybrids, the parental species listed are the hybrids in parentheses, and the latin phrase sedis mutabilis ("changeable position") that is used to mean a polytomy in the cladogram. The cladogram is recovered in the following manner. Section *Pyrethraria* is the sister group of sect. *Anacyclus,* and *A. pyrethrum* and *A. officinarum* are sister taxa within sect. *Pyrethraria* (Fig. 39). In succession; *A. monanthos* is the sister taxon of the remaining species; *A. marocannus* is the sister taxon to the remaining species; *A. radiatus* is the sister taxon to the remaining species; the "clavatus group" is the sister group to *A. latealatus* and *A. nigellifolius* (Fig. 39); within the "clavatus group," *A. linearilobus* is the sister taxa of *A. clavatus* and *A. homogamos* and their two hybrids; and *A. homogamos* is the sister taxon of *A. clavatus,* but forms a polytomy with the two hybrids.

I add to this the provision that should the two parents occur in different subgeneric groups (or different genera) then the hybrid should be listed in both groups.

CONCLUSION

In general, phylogenetic systematics can be used to help identify possible hybrids and their parents for further study. However, several conditions exist in some groups that make a cladistic analysis more difficult. Such conditions include the following: 1) having an increased percentage of species within a group that are hybrids, 2) having hybrids that have mainly plesiomorphies, 3) having hybrids that hybridize with one another, 4) having species that can reproduce asexually, and/or 5) having introgression occur.

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APPENDICES A–S. Only the apomorphies are indicated in the data matrices because in phylogenetic systematics only the apomorphies are used to group taxa.

APPENDIX A. Data matrix for Figure 2.

Taxa	Apomorphies						
	1	2	3	4	5	6	7
A	1		1		1	1	1
B	1		1	1	1	1	1
C	1		1	1			
D	1	1					
E	1						

APPENDIX B. Data matrix for Figures 3–6.

Taxa	Apomorphies				
	1	2	3	4	5
A	1		1		1
B	1		1	1	
C	1	1			
H	1			1	1

APPENDIX C. Data matrix for Figure 7.

Taxa	Apomorphies					
	1	2	3	4	5	6
A	1		1		1	1
B	1		1	1		
C	1	1				
H	1		1	1	1	1

APPENDIX D. Data matrix for Figures 8–12.

Taxa	Apomorphies				
	1	2	3	4	5
A		1	1		1
B	1		1		1
C				1	1
H1	1	1	1		1
H2	1	1	1		1

APPENDIX E. Data matrix for Figure 13.

Taxa	Apomorphies				
	1	2	3	4	5
A	1		1		1
B		1	1		1
C				1	1
H			1		1

APPENDIX F. Data matrix for Figures 14–17, 19.

Taxa	Apomorphies								
	1	2	3	4	5	6	7	8	9
A	1	1							1
B	1		1	1					1
C	1		1		1				1
D						1	1		1
E						1		1	1
H	1		1		1	1	1		1

APPENDIX G. Data matrix for Figure 18.

Taxa	Apomorphies								
	1	2	3	4	5	6	7	8	9
A	1	1							1
B	1		1	1					1
C	1		1		1				1
D						1	1		1
E						1		1	1
H									1

APPENDIX H. Data matrix for Figures 20–22.

Taxa	Apomorphies				
	1	2	3	4	5
A	1	1	1		1
B	1	1	1	1	1
C	1			1	1
D					1

APPENDIX I. Data matrix for Figures 23–25.

Taxa	Apomorphies											
	1	2	3	4	5	6	7	8	9	10	11	12
A	1										1	1
B	1	1										
C	1	1	1									
D	1	1	1	1						1		
E	1	1	1	1	1							
F	1	1	1	1	1	1		1				
G	1	1	1	1	1	1	1		1			
H	1	1	1	1	1	1	1	1	1			
1	1	1	1	1						1	1	1

APPENDIX J. *Microloma* R. Br. (Asclepidaceae). Abbreviations.—A. *M. incanum* Decne.—B. *M. longitubum* Schlechter.—C. *M. burchellii* N. E. Brown.— D. *M. armatum.*—E. *M. campanulatum.*—F. *M. dolichanthum.*—G. *M. spinosum* N. E. Brown.—H. *M. viridiflorum* N. E. Brown.—I. *M. lanatum.* Characters.—Data published in Bremer and Wanntorp (1979) and Humphries (1983) but no character list was furnished in either publication. Data matrix.—For Figures 26, 27, 36–38.

Taxa	Apomorphies						
	1	2	3	4	5	6	7
A							1
B	1					1	1
C	1	1	1	1	1	1	1
D		1	1	1	1	1	1
E			1	1	1	1	1
F				1	1	1	1
G				1	1	1	1
H					1	1	1
1					1	1	1

APPENDIX K. Data matrix for Figures 28, 29.

Taxa	Apomorphies												
	1	2	3	4	5	6	7	8	9	10	11	12	13
A	1	1		1		1		1					
B	1	1		1		1	1						
C	1	1		1	1								
D	1	1	1										
E	1								1	1			
F	1								1		1	1	
G	1								1		1		1
H	1	1				1						1	

APPENDIX L. Data matrix for Figures 30, 31.

Taxa	Apomorphies								
	1	2	3	4	5	6	7	8	9
A	1	1							1
B	1		1	1					1
C	1		1		1				1
D						1	1		1
E						1		1	1
H	1			1	1	1			1

APPENDIX M. Data matrix for Figures 32, 33.

Taxa	Apomorphies												
	1	2	3	4	5	6	7	8	9	10	11	12	13
A	1	1	1	1	1	1							1
B	1	1	1	1	1		1						1
C	1	1	1	1					1	1			1
D											1	1	1
E											1	1	1
H	1	1		1				1			1		1

APPENDIX N. *Anacyclus* L. (Asteraceae, Anthemideae). Abbreviations.—A. *A. pyrethrum* (L.) Link var. *pyrethrum.*—B. *A. pyrethrum* (L.) Link var. *depressus* (Ball) Maire.—C. *A. monanthos* (L.) Thell.—D. *A. maroccanus* (Ball) Ball.—E. *A. radiatus* Loisel.—F. *A. coronatus* (Murb.) Humphries.—G. *A. clavatus* (Desf.) Pers.— H. *A. homogamos* (Maire) Humphries.—I. *A. valentinus* L.—J. *A. inconstans* Pomel.—K. *A. linearilobus* Boiss. & Reuter.—L. *A. latealatus* Hub.-Mor.—M. *A. nigellifolius* Boiss.—N. *A. officinarum* Hayne. Characters.— Published in Humphries (1979). Data matrix.—Lower case letters represent groups of characters that display that pattern so that there are five apomorphies that have the distribution patterns of *a*, etc. For Figures 39–43.

Taxa	Apomorphies																
	a (5)	b (3)	c (1)	d (3)	e (3)	f (1)	g (3)	h (1)	i (1)	j (1)	k (1)	l (1)	m (3)	n (5)	o (4)	p (1)	q (1)
AB	1													1	1	1	1
C	1	1	1													1	1
D	1	1	1	1													
EF	1	1	1	1	1	1				1							
G	1	1	1	1	1	1	1	1	1			1					
H	1	1	1	1	1	1	1	1	1		1						
I	1	1	1	1	1	1	1	1	1		1	1					
J	1	1	1	1	1	1	1	1	1		1	1					
K	1	1	1	1	1	1	1	1									
LM	1	1	1	1	1	1	1						1				
N	1	1				1									1		1

APPENDIX O. *Agastache* Clayt. (Lamiaceae). Abbreviations.—aur. *A. aurantiaca* (A. Gray) Lint & Epling.—brv. *A. breviflora* (A. Gray) Epling.—can. *A. cana* (W. J. Hooker) Wooton & Standley.—coc. *A. coccinea* (Greene) Lint & Epling.—epl. *A. eplingiana* R. Sanders.—mex. *A. mexicana* (H.B.K.) Lint & Epling.—mic. *A. micrantha* (A. Gray) Wooton & Standley.—mrn. *A. mearnsii* Wooton & Standley.—ne-h. *A. pallidiflora* (Heller) Rydberg subsp. *neomexicana* (Briquet) Lint & Epling var. *havardii* (A. Gray) R. Sanders.—ne-n. *A. pallidiflora* (Heller) Rydberg subsp. *neomexicana* (Briquet) Lint & Epling var. *neomexicana*.—pd-c. *A. pallida* (Lindley) Cory var. *coriacea* R. Sanders.—pd-p. *A. pallida* (Lindley) Cory var. *pallida*.—pf-r. *A. pallidiflora* (Heller) Rydberg subsp. *pallidiflora* var. *greenei* (Briquet) R. Sanders.—pf-i. *A. pallidiflora* (Heller) Rydberg subsp. *pallidiflora* var. *gilensis* R. Sanders.—pf-p. *A. pallidiflora* (Heller) Rydberg subsp. *pallidiflora*.—plm. *A. palmeri* (B. L. Robinson) Lint & Epling.—prn. *A. pringlei* (Briquet) Lint & Epling.—rup. *A. rupestris* (Greene) Standley.—wrt. *A. wrightii* (Greenmax) Wooton & Standley. Characters.—As published in Sanders (1981) except for the removal of apomorphy 7 because it was an autapomorphy for a subspecific taxon not used in this analysis. Data matrix.—For Figures 44–46.

Taxa															Apomorphies																			
	1	2	3	4	5	6	8	9	10	11	12	13	14	16	17	18	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
aur	1	1	1		2				1	2				1	1			2'		1	1	1	1	1a									
brv										1a	1	1		1				1		1													
can	1	1	1		2'				1	1				1				2'		1													
coc										1				1	1			1'										1	1				
epl					1					1				1	1		1	1										1	1				
mex					1					1				1	1		1	1	1						1'								
mic			1	1		1															1												
mrn											1	1		1				1'				1	1							1			
ne-h							1					1	1	1				1			1									1			
ne-n							1					1		1				1			1												
pd-c														1		1		1															
pd-p									1	1				1		1		1			1									1	1		
pf-i								1				1'		1				1												1	1		
pf-p								1				1		1				1			1									1		1	
pf-r								1				1		1				1							1'								
plm									1	1				1				1			1	1						1					
prn										1a		1		1				1			1		1a										
rup	1	1	1	1	2"	1			1	2								2		1	1	1	1			1	1						
wrt																									1	1	1						1

[a] Varies between the apomorphy and plesiomorphy.

APPENDIX P. *Chrysopsis* (Nutt.) Ell. and *Bradburia* Semple & Chinnappa (Asteraceae). Abbreviations.—
BR. *B. hirtella* T. & G.—flo. *C. floridana* Small.—gd-g. *C. godfreyi* Semple f. *godfreyi.*—gd-v. *C. godfreyi*
Semple f. *viridis* Semple.—gs-c. *C. gossypina* (Michx.) Elliot subsp. *cruiseana* (Dress) Semple.—gs-gd. *C. gos-
sypina* (Michx.) Elliot subsp. *gossypina* f. *decumbens* (Chapm.) Godfrey.—gs-gg. *C. gossypina* (Michx.) Elliot
subsp. *gossypina* f. *gossypina.*—gs-gt. *C. gossypina* (Michx.) Elliot subsp. *gossypina* f. *trichophylla* (Nutt.) Semple.—
gs-h. *C. gossypina* (Michx.) Elliot subsp. *hyssopifolia* (Nutt). Semple.—lan. *C. lanuginosa* Small.—lat. *C. la-
tisquamea* Pollard.—li-d. *C. linearifolia* Semple subsp. *dressii* Semple.—li-l. *C. linearifolia* Semple subsp. *li-
nearifolia.*—mar. *C. mariana* (L.) Elliot.—pil. *C. pilosa* Nutt.—sca. *C. scabrella* T. & G.—sub. *C. subulata*
Small. Characters—Original characters furnished by Semple and modified slightly by Funk.

	Transformation Series	Plesiomorphic Character	Apomorphic Character
2A.	Growth form	biennial	perennial
2B.	Growth form	biennial	annual
4.	Pubescence of basal rosettes	wooly	pilose
6.	Achene body	no translucent ribs	translucent ribs
7A.	Outer pappus	bristles narrow	bristles broad
7B.	Outer pappus	present	absent
8.	Upper cauline leaves	wooly	not wooly
9.	Glandulation of upper cauline leaves	sparsely	densely
10.	Upper leaf base	sessile, nonclasping	clasping
11.	Upper leaf size	not greatly reduced	greatly reduced
12.	Glandulation of peduncles	glandular	eglandular
13.	Upper leaf shape	elliptic	linear
14.	Upper leaf apex	obtuse	acute
15.	Glandulation of phyllaries	densely	eglandular
16.	Pubescence of phyllaries	glabrate	pubescent
17.	Phyllary size	narrow	broad
18.	Phyllary apex	acute-attenuate	long, subulate
19.	Outer phyllary size	much shorter than inner phyllaries	similar in size
20.	Head orientation in bud	erect	nodding
21.	Inflorescence type	open cymose	subumbellate
22.	Heads/inflorescence branch	few	many
23.	Disc florets	hemaphroditic	staminate

Data matrix.—For Figures 47–50.

	Apomorphies																						
Taxa	2A	2B	4	5	6	7A	7B	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
BR		1	1	1		1	1	1		1		1	1	1									1
flo		1																		1			
gd-g		1										1						1	1				
gd-v		1				1	1	1				1						1	1				
gs-c	1				1			1				1			1						1		
gs-gd																							
gs-gg			1									1		1		1							
gs-gt			1					1				1		1									
gs-h	1		1		1			1				1	1	1							1		
lan						1	1	1					1					1	1			1	
lat				1													1						
li-d				1				1				1		1									
li-l				1				1			1	1		1								1	
mar		1	1	1				1		1											1		
pil		1	1	1			1	1		1	1												
sca								1	1			1											
sub					1			1				1		1	1	1		1	1		1		

APPENDIX Q. *Encelia* Adanson (Asteraceae). Abbreviations.—act. *E. actoni* Elmer.—asp. *E. asperifolia* (S. F. Blake) Clark & Kyhas.—cal. *E. californica* Nutt.—can. *E. canescens* Cav.—far. *E. farinosa* Gray.—fru. *E. frutescens* Gray.—GC. Undescribed taxon from Grand Canyon (C. Clark, pers. comm.).—lac. *E. laciniata* Vasey & Rose.—pal. *E. palmeri* Vasey & Rose.—phe. *E. farinosa* Gray var. *phenicodonta* I. M. Johnston.—rad. *E. radians* Brandegee.—rav. *E. ravenii* Wiggins.—res. *E. resinosa* Brandegee.—SC. Undescribed taxon from Picachos de Santa Clara, Baja (C. Clark, pers. comm.).—SF. Undescribed taxon from San Felipe (C. Clark, pers. comm.).—ven. *E. ventorum* Brandegee.—vir. *E. virginensis* Nelson. Characters.—To be published by Clark (pers. comm.). Data matrix.—For Figures 51–54.

Taxa	Apomorphies															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
act																1
asp	1	1			1			1	1							
cal	1	1			1			1				1				
can	1	1	1		1		1	1				1		1		
GC								1			1				1	
far					1		2ᵃ					1		2		
fru						1		1			1	1			1	
lac	1	1	1		1			1		1			1			
pal	1	1	1		1		1	1				1				
phe	1	1	1		1		2ᵃ					1		2		
rad	1	1	1		1		2ᵃ									
rav				1											1	
res								1							1	
SC		1			1							1	1			1
SF						1		1			1				1	
ven	1	1	1		1			1		2			1			1
vir									1							

ᵃ Varies between apomorphies 2 and 1.

APPENDIX R. *Montanoa* Cerv. (Asteraceae). Abbreviations.—AN. *M. andersonii* McVaugh.—AG. *M. angulata* Badillo.—AT. *M. atriplicifolia* (Pers.) Sch. Bip.—B. *M. bipinnatifida* (Kunth) K. Koch.—E. *M. echinacea* S. F. Blake.—F. *M. fragrans* Badillo.—FU. *M. frutescens* DC.—GA. *M. grandiflora* DC.—G. *M. guatemalensis* Robins. & Greenm.—HE. *M. hexagona* Robins. & Greenm.—H. *M. hibiscifolia* Benth.—I. *M. imbricata* V. A. Funk.—J. *M. josei* V. A. Funk.—K. *M. karwinskii* DC.—L. *M. laskowskii* McVaugh.—LE. *M. leucantha* (Lag.) S. F. Blake.—LI. *M. liebmannii* (Sch. Bip.) S. F. Blake.—M. *M. mollissima* Groenland.—O. *M. ovalifolia* DC.—P. *M. pteropoda* S. F. Blake.—Q. *M. quadrangularis* Sch. Bip.—R. *M. revealii* H. Robinson.—S. *M. speciosa* DC.—ST. *M. standleyi* V. A. Funk.—T. *M. tomentosa* Cerv. Characters.—Published in Funk (1982). Data matrix.—For Figure 55.

Taxa	Apomorphies																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19	20	21	22
AN		1	1					1	1					1							
AG	1			1	1	1	1														
AT	1			1	1	1	1														
B	1			1	1	1	1														1
E		1	1					1	1				1			1	1				1
F	1			1	1	1	1												1		
FU		1	1					1	1					1							
GA	1			1	1	1	1														1
G		1	1					1	1					1				1	1	1	
HE	1			1	1	1	1														
H	1			1	1	1	1											1			
I	1			1	1	1	1														1
J	1			1	1	1	1														
K	1			1	1	1	1														
L	1			1	1	1	1												1		
LE	1			1	1	1	1														
LI		1	1					1	1				1			1	1				
M		1	1					1	1					1				1	1		
O	1			1	1	1	1														1
P	1			1	1	1	1														
Q	1			1	1	1	1														
R		1	1					1	1				1		1						
S	1			1	1	1	1														1
ST		1	1					1	1					1							
T		1	1							1	1	1									

APPENDIX R. Continued.

Apomorphies																							
23	24	25	26	27	28	29	30	31	32	34	35	36	37	38	39	40	41	42	43	44	45	46	47
			1	1		1						1											
																				1			
										1	1					1			1				
1	1		1			1									1	1	1			1			
1	1	1	1		1		1	1															
	1																1		1				
		1																					
1	1		1			1										1	1	1					
		1																					
											1					1				1	1		
										1	1		1			1			1	1	1		
1	1		1			1					1					1	1	1	1				
											1	1				1				1			
1	1									1	1			1		1							
1	1		1								1					1							
										1						1							
1	1	1	1		1		1	1															
		1																					
	1																1	1	1				
				1			1	1		1	1					1			1				
												1								1			
			1				1	1															1
1	1		1			1										1	1	1	1			1	
			1						1														

APPENDIX S. *Acmella* Rich. ex Pers. (Asteraceae). Abbreviations (* indicates chromosome number is an estimate from pollen diameter).—1. *A. poliolepidica* (A. H. Moore) R. K. Jansen (4*x*).—2. *A. pilosa* R. K. Jansen (2*x*).—3a. *A. oppositifolia* Rich. var. *repens* (Walt.) R. K. Jansen (4*x*).—3b. *A. oppositifolia* Rich. var. *oppositifolia* (2*x*, 3*x*, 4*x*, 5*x*, 6*x*).—4. *A. ciliata* (H.B.K.) Cass. (6*x*).—5. *A. caulirhiza* Delile (2*x*).—6. *A. calva* (DC.) R. K. Jansen (4*x**).—7. *A. darwinii* (D. M. Porter) R. K. Jansen (6*x**).—8. *A. sodiroi* (Hieron) R. K. Jansen (6*x*).—9. *A. ramosa* (Hensl.) R. K. Jansen. (2*x*).—10. *A. pusilla* (Hook. & Arn.) R. K. Jansen (2*x*, 4*x*).—11. *A. lundellii* R. K. Jansen (2*x**).—12a. *A. papposa* (Hemsl.) R. K. Jansen var. *papposa* (4*x*).—12b. *A. papposa* (Hensl.) R. K. Jansen var. *macrophylla* (Greenm.) R. K. Jansen (4*x*).—13. *A. iodiscaea* (A. H. Moore) R. K. Jansen (4*x*).—14. *A. uliginosa* (Sw.) Cass. (4*x*).—15a. *A. filipes* (Greenm.) R. K. Jansen var. *filipes* (2*x**).—15b. *A. filipes* (Greenm.) R. K. Jansen var. *cayensis* R. K. Jansen (2*x**).—15c. *A. filipes* (Greenm.) R. K. Jansen var. *parvifolia* (Benth.) R. K. Jansen (2*x*).—16a. *A. alba* (L'Herit.) R. K. Jansen var. *alba* (6*x**).—16b. *A. alba* (L'Herit.) R. K. Jansen var. *ecuadorensis* R. K. Jansen (6*x**).—18. *A. leucantha* (H.B.K.) R. K. Jansen (6*x**).—19. *A. paniculata* (DC.) R. K. Jansen (4*x**).—20a. *A. radicans* (Jacq.) R. K. Jansen var. *radicans* (6*x*).—20b. *A. radicans* (Jacq.) R. K. Jansen var. *devilis* (H.B.K.) R. K. Jansen (6*x*).—21. *A. brachyglossa* Cass. (6*x*).—22a. *A. grandiflora* (Turcz.) R. K. Jansen var. *grandiflora* (4*x**).—22b. *A. grandiflora* (Turcz.) R. K. Jansen var. *brachyglossa* (Benth.) R. K. Jansen (4*x*).—22c. *A. grandiflora* (Turcz.) R. K. Jansen var. *discoidea* R. K. Jansen (6*x**).—23a. *A. decumbens* (Smith) R. K. Jansen var. *decumbens* (4*x*).—23b. *A. decumbens* (Smith) R. K. Jansen var. *affinis* (Hook. & Arn.) R. K. Jansen (2*x*).—24. *A. leptophylla* (DC.) R. K. Jansen (2*x*).—25. *A. bellidioides* (Smith) R. K. Jansen (2*x*).—26. *A. grisea* (Chodat) R. K. Jansen (2*x*).—27. *A. serratifolia* R. K. Jansen (2*x*).—28. *A. alpestris* (Griseb.) R. K. Jansen (2*x*).—29. *A. psilocarpa* R. K. Jansen (2*x**).—30. *A. glaberrima* (Hassler) R. K. Jansen (2*x*). Characters.—Taken from Jansen (in press) with the following changes: transformation series 13–15 were eliminated because I felt they were the same as 20–22; transformation series 11 and 12 were combined into one transformation series with two independent apomorphies. Data matrix.—The apomorphies of transformation series 8, 11, and 21 were all treated as independent of one another while in transformation series 2, 17, and 18, apomorphy 1 is of intermediate nature between the plesiomorphic character and the other apomorphy, 2. For Figure 56.

| Taxa | Apomorphies | | | | | | | | | | | | | | | | | |
	1	2	3	4	5	6	7	8	9	10	11	16	17	18	19	20	21	22
1						1										1		1
2		1	1		1			1								1		1
3a		1	1							1						1	1	1
3b		1	1													1	3	1
4		1	1	1							1					1		
5		1	1						1		1		1			1	3	1
6		1	1								2					1	3	1
7		1	1	1							2		2	2		1	3	1
8		1	1								2			2		1	3	1
9		2	1															1
10		2	1			1										1	2	1
11		2	1			1											2	1
12a		1	1								1							1
12b								1			1							1
13	1							2		1	1	1	1	2				1
14	1							2			1		2					1
15a	1							2										1
15b	1																	
15c	1							2										
16a	1									1	2	1		2				1
16b	1									1	2							1
18	1										2			2			3	1
19	1										2		1	2				
20a	1										2		2	2				1
20b	1										1		2	2				
21	1										1		1	1				1
22a				1			1	1		1								1
22b				1		1	1	1							1			1

APPENDIX S. Continued.

Taxa	Apomorphies																	
	1	2	3	4	5	6	7	8	9	10	11	16	17	18	19	20	21	22
22c				1			1				2				1			1
23a		1	1			1	1											1
23b				1		1	1											1
24				1		1	1											1
25				1			1											1
26				1			1											1
27				1			1											1
28				1			1									1	3	1
29				1			1									1	3	1
30				1		1	1	1								1	2	