TAXON 34(1): 72–80. FEBRUARY 1985

# CLADISTICS AND GENERIC CONCEPTS IN THE COMPOSITAE

*V. A. Funk*[1]

*Summary*

Cladistic classifications seek to recognize monophyletic groups while changing the existing nomenclature as little as possible. When applied to the discussion of generic concepts this approach means that new descriptions and combinations are justifiable only when they are necessary for the delimitation of natural groups of species (monophyletic groups, sensu Hennig).

## *Introduction*

Taxonomy classes are often taught that we as systematists are concerned with grouping and ranking. We are actually concerned with two levels of grouping: the grouping of individuals (into species), and the grouping of these "groups of individuals." There are, therefore, only two categories, species and groups of species (Nelson and Platnick, 1981). If we strive to make our species represent the units of evolution, then all higher ranking categories are really just monophyletic groups of species, no matter what we choose to call them. The importance of this concept lies in a logical extension of it: as long as they are natural, the various levels at which the "groups of species" are recognized are not of major concern to cladists. However, as is evidenced by my use of the qualifier "natural," we are concerned with the quality of the groups.

It is not my intention to discuss cladistic methodology in this paper because many publications are available that accomplish this task (e.g., Eldredge and Cracraft, 1980; Hennig, 1966; Humphries and Funk, 1984; Nelson and Platnick, 1981; Wiley, 1981). However, it is necessary to explain a few terms. First, the term "apomorphy" has been variously defined as a unique character (Platnick, 1979) and as an evolutionary novelty (Wiley, 1981). What these definitions attempt to convey is the concept of a derived character that is shared by one or more taxa because of common descent. A "synapomorphy" is an apomorphy shared by more than one terminal taxon and an "autapomorphy" is characteristic of a single terminal taxon. For instance, in a cladogram of *Tetragonotheca* L. (Fig. 1; Seaman and Funk, 1983) there is a synapomorphy that unites the terminal taxa *T. texana* Gray & Engelm. and *T. repanda* Small, and a second synapomorphy that unites *T. ludoviciana* Gray and *T. helianthoides* L.

Second, the terms "clade," "monophyletic group," and "natural group" all mean the same thing: a group that includes all taxa above a synapomorphy on the cladogram. These may also be defined as all descendents of a common ancestor. Such groups are regarded as natural because they represent a unit that has a common evolutionary history. In Fig. 2, the angiosperms and gymnosperms form a monophyletic group because they are defined by at least one synapomorphy. Likewise, the angiosperms, gymnosperms and ginkgos form a monophyletic group. The third monophyletic group on this cladogram contains all four taxa, the angiosperms, gymnosperms, ginkgos and cycads. Groups that do not fulfill the requirement for being clades are either paraphyletic or polyphyletic. Paraphyletic taxa are those that are defined only by plesiomorphies (characters that are not unique or novel at

[1] Department of Botany, Smithsonian Institution, Washington, DC 20560, U.S.A.

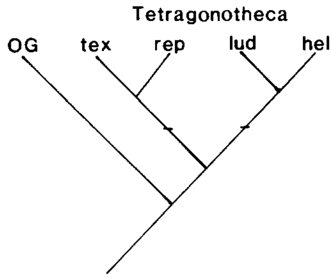



*Fig. 1.* *Tetragonotheca* sesquiterpene lactone cladogram. hel = *T. helianthoides*, lud = *T. ludoviciana*, rep = *T. repanda*, tex = *T. texana*, OG = outgroup. Redrawn from Seaman and Funk (1983).

that level of the cladogram). All members of a paraphyletic taxon have a common ancestor but the group is not monophyletic because it does not contain all possible members of the clade (Fig. 3, Group C; Fig. 4, Groups D and E). Polyphyletic groups contain taxa from more than one clade and exclude their common ancestor (Fig. 4, Group F). Monophyletic groups are Groups A and B in Fig. 3. Returning to Fig. 2, putting either the gymnosperms, cycads and ginkgos together in one group or the cycads and ginkgos together in one group creates paraphyletic taxa. Certain examples can be constructed in which polyphyletic and paraphyletic taxa cannot be distinguished (S. Farris, 1982, pers. comm.), but the important point for this discussion is that neither is monophyletic.

To discuss generic concepts, we begin with a properly constructed cladogram in which species are the terminal taxa. How do we convert this cladogram into genera? To cladists, the cladogram is the classification, and the guideline for turning it into a hierarchy is as follows: while maximizing information, strive to minimize novelty (modified from Wiley, 1979). The goal is to develop a classification that will recognize monophyletic groups but disrupt the present classification as little as possible. The only justification for describing new genera is to develop a system of classification that contains monophyletic groups when this was not previously the case. A taxon is not circumscribed from an existing genus unless it is 1) more closely related to species in a different genus, or 2) the group of species on the cladogram is a paraphyletic assemblage that can never be defined because it contains only the "leftover species" that are not "different enough" to have inspired previous treatment at the generic level.

*Some Examples*

Treatments that rely on ease of recognition to delimit genera can lead to two major problems, core genera and artificial genera. Although disruption in the nomenclature is minimized, information is not necessarily maximized by the use of core genera such as

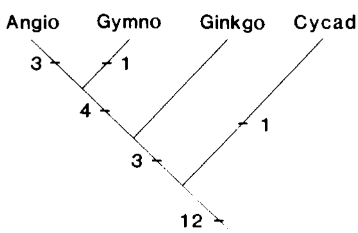
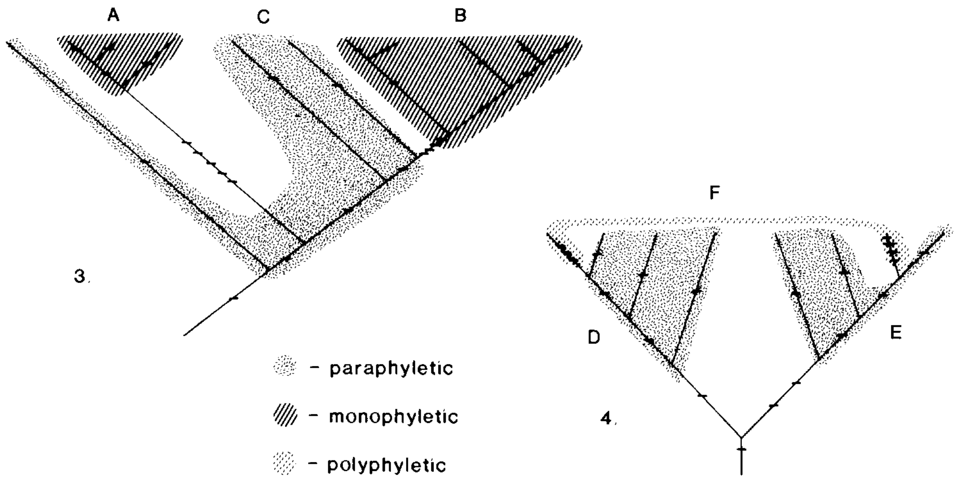



*Fig. 2.* Cladogram showing the relationships among cycads, ginkgos, gymnosperms (Gymno) and angiosperms (Angio). Numbers indicate the total number of synapomorphies at the internode. Redrawn from Humphries and Funk (1984).




*Figs. 3, 4.* Cladograms illustrating the definitions of monophyletic, paraphyletic and polyphyletic groups.

*Vernonia* Schreb., *Senecio* L., and *Eupatorium* L., over smaller monophyletic groups (Cronquist, 1977; Turner, 1981). However, this is not a *carte blanche* for describing new genera, because the segregates must be defined by synapomorphies and the parent group cannot be left paraphyletic. An example is found in the segregation of *Metastevia* Grashoff from *Stevia* Cav. (Grashoff, 1975). A monophyletic group has been recognized (Fig. 5; *Metastevia*) but a paraphyletic group has been left behind (Fig. 5; *Stevia*). All synapomorphies that delimit *Stevia* also delimit *Metastevia*, and there is no information about the evolution of *Stevia* that is not also true of its segregate. *Stevia* is a paraphyletic group defined only by plesiomorphies. If one strives for a classification that reflects only natural groups as defined above, then the recognition of *Metastevia* is not acceptable.

Another example of the recognition of segregate genera is in the tribe Liabeae (genera

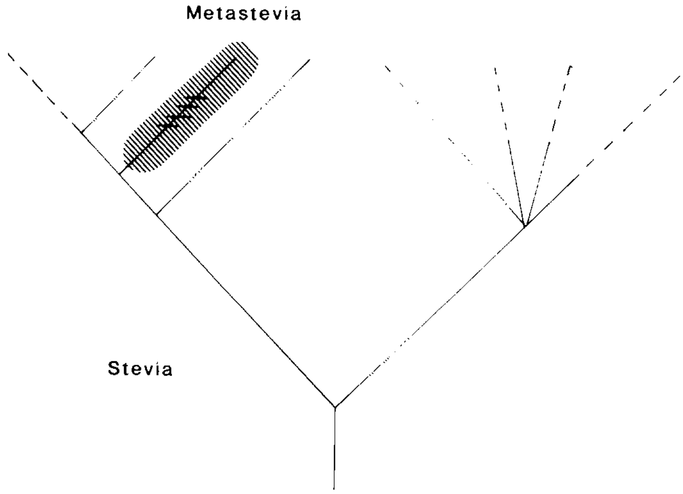



*Fig. 5.* Cladogram illustrating that the recognition of the monophyletic genus *Metastevia* automatically leaves the genus *Stevia* paraphyletic.

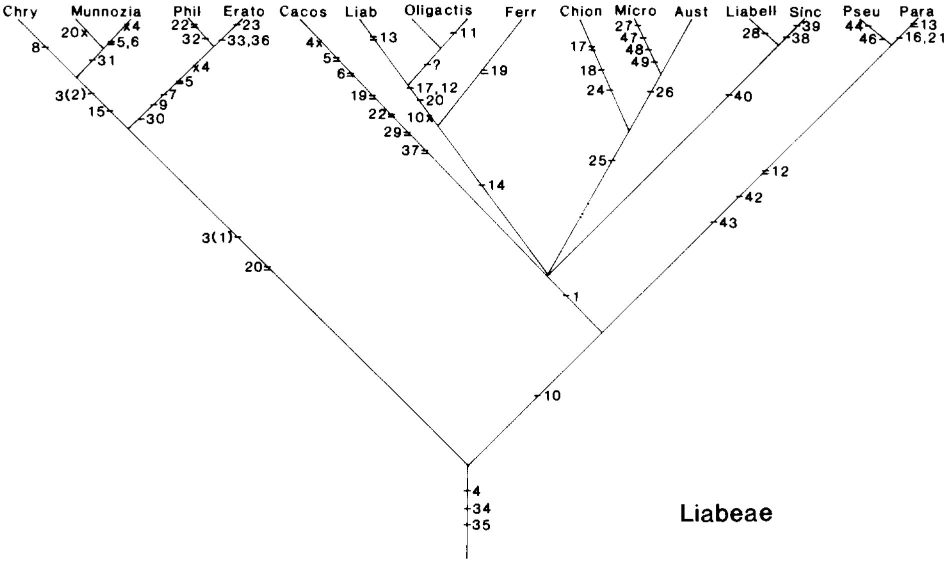



*Fig. 6.* Preliminary cladogram of the tribe Liabeae. Single lines indicate synapomorphies, double lines indicate parallelisms, 'x' indicates the loss of a particular synapomorphy. Aust = *Austroliabum,* Cacos = *Cacosmia,* Chion = *Chionopappus,* Chry = *Chrysactinium,* Ferr = *Ferreyranthus,* Liab = *Liabum,* Liabell = *Liabellum,* Micro = *Microliabum,* Para = *Paranephelium,* Phil = *Philoglossa,* Pseu = *Pseudonoseris,* Sinc = *Sinclairia.*

are those of Robinson, 1983). In a preliminary cladogram of the tribe (Fig. 6; Funk, in prep.) one genus, *Astroliabum* H. Robinson and R. D. Brettel (1974), is not defined by a synapomorphy. Examining it in more detail (Fig. 7), the reason for the lack of a synapomorphy becomes apparent. The monotypic genera *Chionopappus* Bentham and *Microliabum* Cabrera are defined by synapomorphies, but there is no synapomorphy to unite the three species of *Austroliabum* [*A. polymnioides* (R. E. Fries) H. Robinson and Brettell, *A. candidum* (R. E. Fries) H. Robinson and Brettell, and *A. eremophilum* (Cabrera) H. Robinson and Brettell]. Therefore, the genus *Austroliabum* is paraphyletic. Based on character information available at this time, *Austroliabum* should have been placed in *Microliabum,*

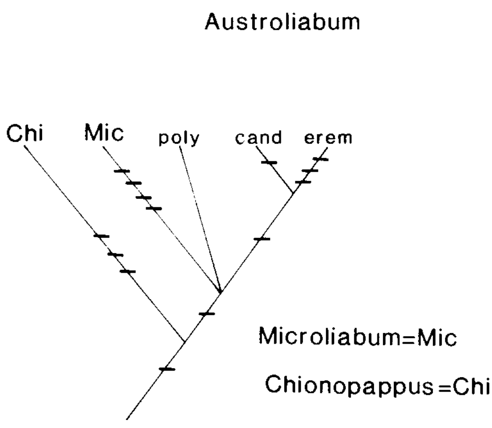



*Fig. 7.* Cladogram of *Austroliabum, Microliabum* and *Chionopappus.* Lines indicate synapomorphies. poly = *A. polymnioides,* cand = *A. candidum,* erem = *A. eremophilum.*

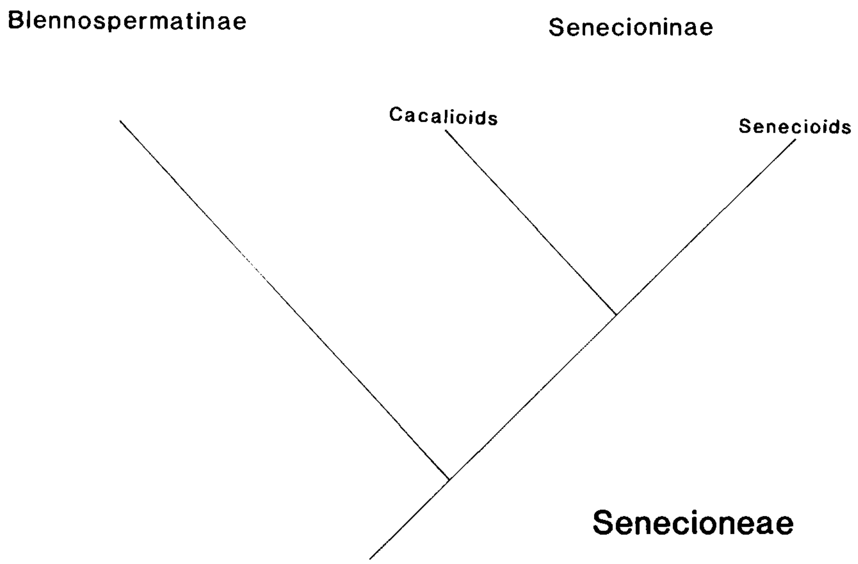



*Fig. 8.* Cladogram of the tribe Senecioneae showing the relationship between the two subfamilies Blennospermatinae and Senecioninae and the two informal groups within the Senecioninae, the Cacalioids and Senecioids.

or both genera could have been placed in *Chionopappus* (see Fig. 6), to maintain monophyletic genera.

The tribe Senecioneae can be used as an example of a group that has paraphyletic, monophyletic and polyphyletic groups of species. There are three major groups in the tribe, the Blennospermatinae, and the Senecioids and the Cacalioids within the Senecioninae (Fig. 8). The Blennospermatinae is probably a paraphyletic assemblage of so-called "primitive genera" that do not belong in either of the other two groups. Within the Cacalioids there are approximately 20 genera, of which most appear to be natural. Some of the genera

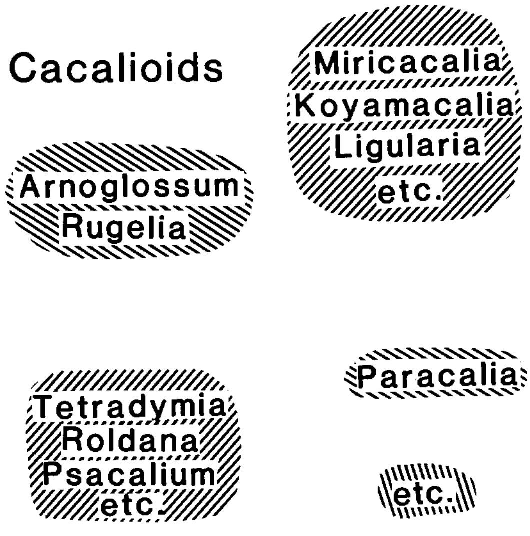



*Fig. 9.* Diagram of some of the generic relationships within the Cacalioids.

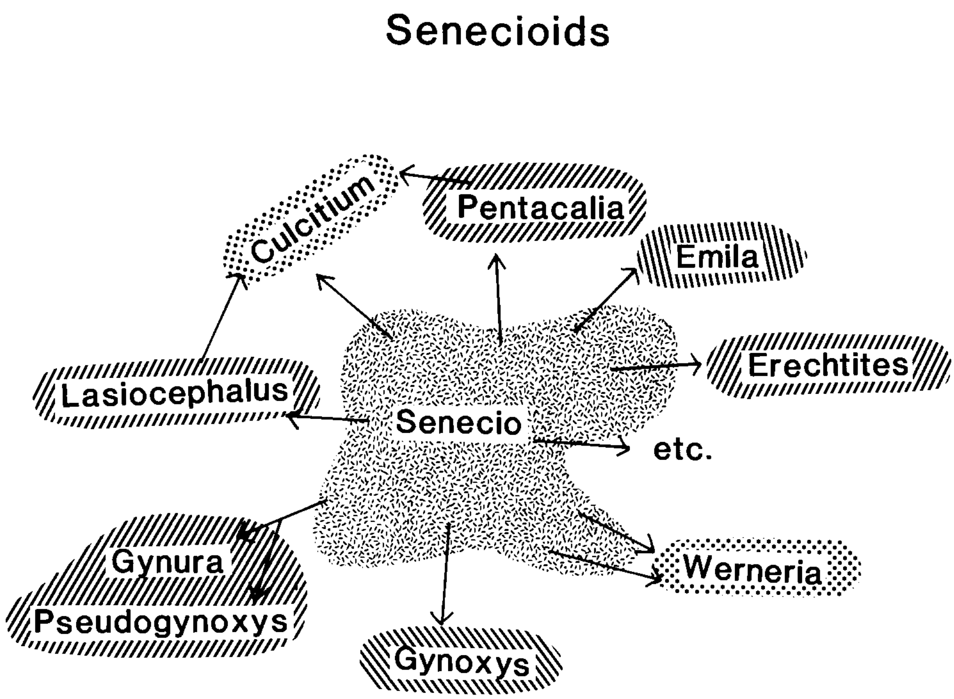



*Fig. 10.* Diagram of some of the generic relationships within the Senecioids.

can be grouped together, but we do not as yet have a good idea of how these groups are related; therefore, one or more are potentially paraphyletic (Fig. 9).

Within the Senecioids, however, the picture is very different (Fig. 10). The large (approximately 1500 species) and apparently paraphyletic genus *Senecio* L. has numerous segregates, such as *Erechtites* Rafin. and *Emilia* Cass., which are clearly monophyletic. Other genera within the Senecioid assemblage, such as *Werneria* Kunth and *Culcitium* Humb. & Bonpl., appear to be polyphyletic. Polyphylesis sometimes results from the practice of defining genera on the basis of one easily recognizable character, as in *Culcitium,* which has been defined traditionally by its calyculus, and *Werneria* recognized by its fused involucral bracts. Maintaining such genera, regardless of ease of identification, is cladistically indefensible because it implies the false information that the species are more closely

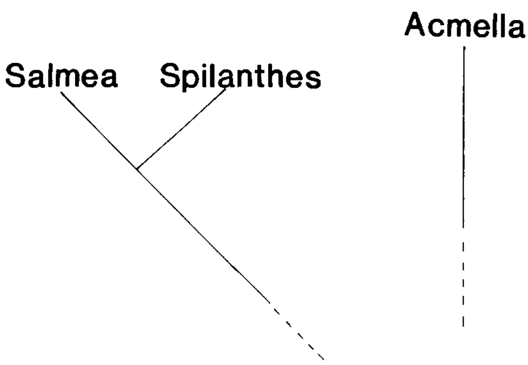



*Fig. 11.* Relationships among *Salmea, Spilanthes* and *Acmella.*

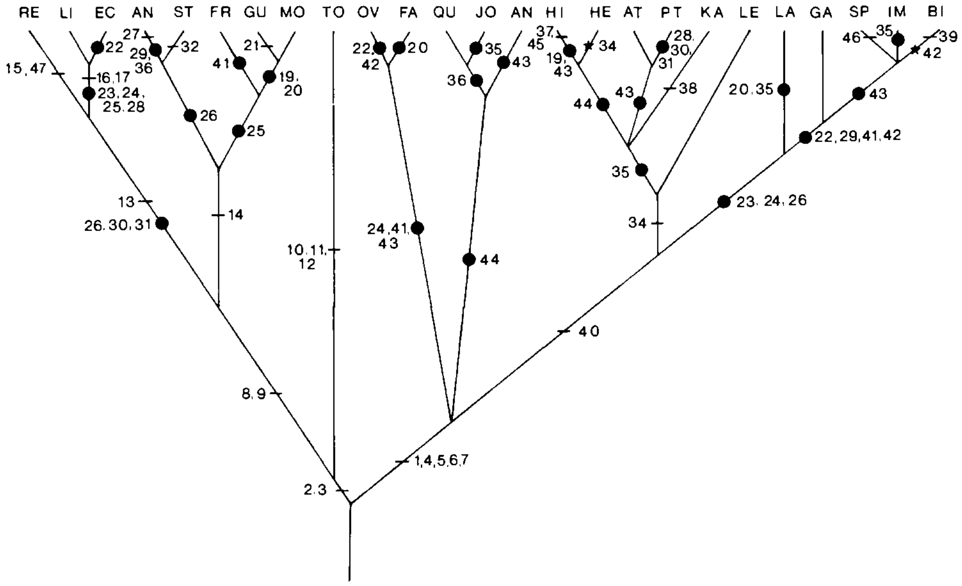



*Fig. 12.* Cladogram of *Montanoa* (Funk, 1982). Lines indicate synapomorphies, closed circles indicate parallelisms, 'x' indicates the loss of a particular synapomorphy.

related to one another than they are to any other species. Cuatrecasas recognized the artificiality of *Culcitium,* transferred some of the species to *Senecio,* and put the remaining ones into either *Pentacalia* Cass. or *Lasiocephalus* Willd. ex Schlecht. (Cuatrecasas, 1978). I am currently revising *Werneria,* which appears to contain at least two different groups of species, of which the typical element seems to be more closely related to *Senecio.* If these taxa are returned to *Senecio,* then a new genus may be needed to accommodate the remaining species.

The category "genus" signifies a group of species more closely related to one another than any are to other species. The members of "genera" that do not fit this description should be taxonomically redistributed. Jansen, in his revision of *Spilanthes* Jacq. (1982), found that that genus actually contained two evolutionary units, the smaller genus *Spilanthes* and a larger group of species that constituted the genus *Acmella* Rich. The original *Spilanthes* was not a monophyletic unit. The species of *Spilanthes* sensu stricto are more closely related to *Salmea* DC. than to the species assigned to *Acmella* (Fig. 11). Clearly, Jansen had no choice but to resurrect this second genus. He legitimately could have placed the species of *Spilanthes* sensu stricto within *Salmea,* but some of the species of that genus, especially the ones from Cuba, are not well collected and are poorly understood and it seemed better to keep them separate until more information becomes available.

The opposite extreme is found in *Espeletia* Mutis, which is a monophyletic group of about 150 species. This has recently been treated as seven genera (Cuatrecasas, 1976). All of these segregates appear to be monophyletic, but so was the original, inclusive, genus. No information has been gained that could not have been expressed by treating the species-groups as subgenera; further, a large number of nomenclatorial changes were necessary in Cuatrecasas' treatment. From a cladistic standpoint, even though they recognized clades, the changes were unnecessary.

A taxonomist may encounter difficulties in an attempt to use the amount of morphological distance (how different things are from one another) as a guideline. Within the cladogram for *Montanoa* (Fig. 12), there are at least three clades, each defined by many synapomorphies, that could easily be defined as genera. Certainly they are better defined than many

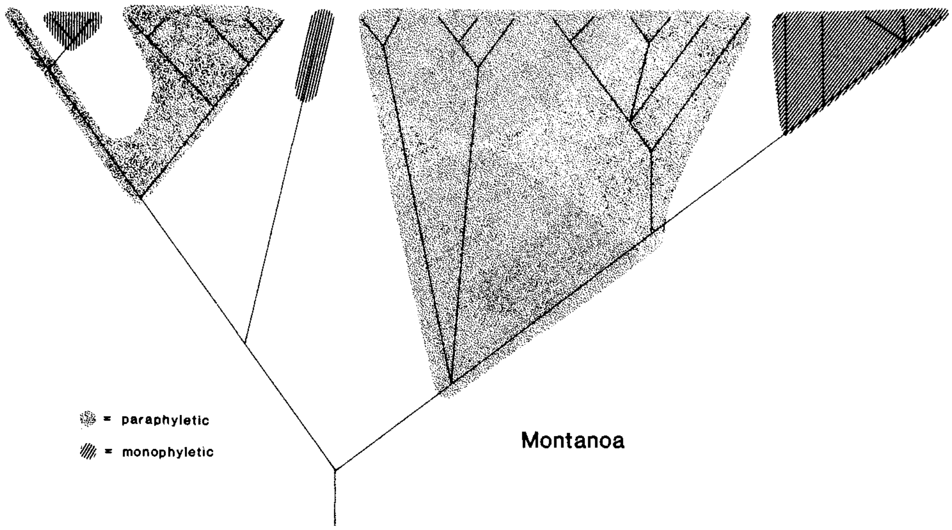



*Fig. 13.* Cladogram showing the result if *Montanoa* were treated as several genera based on the amount of difference found among various clades.

genera in the Heliantheae; indeed the genus *Montanoa* is distinct enough to be a subtribe (Robinson, 1978; Funk, 1982). However, distributing the species of *Montanoa* in this way would leave large, undefinable (non-monophyletic) groups (Fig. 13). The information gained from such a treatment of *Montanoa* would be overwhelmed by the information lost because 1) two large paraphyletic groups would be formed, and 2) many nomenclatural changes would be necessitated. In addition, the large paraphyletic groups would be implied to be evolutionary units, which is untrue.

*Conclusion*

Classifications giving consistent information cannot be achieved by whim. The cladistic approach provides well-reasoned guidelines for evaluating and comparing classifications, and it can aid in making decisions about the retention of existing genera or description of new ones. The comment that the major goal of taxonomy is to group taxa so that they can be identified is answered by the cladistic rule that all groups must be defined by a unique set of characters. Such a statement cannot be made about many of the genera that are currently in use in the Compositae. Since Darwin, taxonomists have sought to reflect the pattern of evolution in their classifications. If classifications are to be employed in the study of relationships, biogeography, coevolution, speciation, or many other interesting subjects, we must strive to identify and recognize monophyletic groups. The fear has been expressed that the introduction of cladistic principles into Compositae classification will lead to the splitting of easily recognizable groups of species into many splinter genera. From the discussion above, it now should be apparent that the use of cladistics does not automatically result in the splitting of genera. To a cladist the question is not "small" or "large" but rather the search for and recognition of monophyletic groups that reflect the pattern of evolution.

*Acknowledgments*

I thank A. Cronquist, B. L. Turner and especially H. Robinson for their conversations with me on the Compositae. For the hours of discussion that I have had with J. Cracraft, D. Hull, G. Nelson, N.

Platnick and E. O. Wiley on, among other things, the subject of "species and groups of species," I can only say, "thanks."

*Literature Cited*

Cronquist, A. 1978. The Compositae revisited. *Brittonia* 29: 137–153.

Cuatrecasas, J. 1976. A new subtribe in the Heliantheae (Compositae): Espeletiinae. *Phytologia* 36: 43–61.

———. 1978. Studies on neotropical Senecioneae, Compositae. I. Reinstatement of genus *Lasiocephalus*. *Phytologia* 40: 307–312.

Eldredge, N. and J. Cracraft. 1980. *Phylogenetic patterns and the evolutionary process.* Columbia Univ. Press, New York.

Funk, V. A. 1982. The systematics of *Montanoa* (Asteraceae, Heliantheae). *Mem. New York Bot. Gard.* 36: 1–133.

Grashoff, J. L. 1975. *Metastevia* (Compositae: Eupatorieae): A new genus from Mexico. *Brittonia* 27: 69–73.

Hennig, W. 1966. *Phylogenetic systematics.* Univ. of Illinois Press, Urbana.

Humphries, C. J. and V. A. Funk. 1984. Cladistic methodology. *In:* V. H. Heywood (ed.), *Modern methods in plant systematics.* Academic Press, London.

Jansen, R. K. 1981. Systematics of *Spilanthes* (Compositae: Heliantheae). *Syst. Bot.* 6: 231–257.

Nelson, G. and N. Platnick. 1981. *Systematics and biogeography: Cladistics and vicariance.* Columbia Univ. Press, New York.

Platnick, N. 1979. Philosophy and the transformation of cladistics. *Syst. Zool.* 28: 537–546.

Robinson, H. 1978. Studies in the Heliantheae (Asteraceae). XV. Various new species and combinations. *Phytologia* 41: 33–44.

———. 1983. A generic review of the tribe Liabeae (Asteraceae). *Smithsonian Cont. Bot.* 54: 1–69.

——— and R. D. Bretell. 1974. Studies in the Liabeae (Asteraceae), II: Preliminary survey of the genera. *Phytologia* 28: 43–63.

Seaman, F. and V. A. Funk. 1983. Cladistic analysis of complex natural products: Developing transformation series from sesquiterpene lactone data. *Taxon* 32: 1–27.

Turner, B. L. 1981. New species and combinations in *Vernonia* sections *Leiboldia* and *Lepidonia* (Asteraceae), with a revisional conspectus of the groups. *Brittonia* 33: 401–412.

Wiley, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* 28: 308–377.

———. 1981. *Phylogenetics: The theory and practice of phylogenetic systematics.* Wiley-Interscience, New York.