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Character States, Morphological Variation, and Phylogenetic Analysis: A Review

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ABSTRACT. The step in cladistic analysis that has received least attention is delimitation of character states, there usually being little justification for their delimitation. It is generally assumed that states of cladistic characters are discrete, even when variation is quantitative. I show here that a majority of the character states of obviously quantitative characters used in lower-level cladistic studies in botany over the last generation are ambiguous even when ingroup variation alone is analyzed. Consideration of variation in the outgroup may compromize either the states recognized in the ingroup and/or the polarity that they are subsequently assigned. Furthermore, many so-called qualitative characters are based on a quantitative phenomenological base filtered through the reified semantic discontinuities of botanical terminology; such characters face the problems of their more obviously quantitative relatives. Methods for delimiting states within quantitative characters are examined. Some produce gaps in the variation by redefining the character, scoring the intermediates in a distinctive fashion, performing phylogenetic analyses within the terminal taxa, or changing the hierarchical level at which the variation is evaluated. Others produce states by manipulation of the statistical properties of the variation of the ensemble of taxa being studied. These latter methods often allow greater resolution of the phylogeny, but at the cost of lowering the significance of the most parsimonious tree. The underlying assumptions of the two sets of methods are briefly analyzed. Problems manifest in the division of continuous variation into character states suggest a reappraisal of the early steps of cladistic analysis; in practice, character states often seem to be delimited in conjunction with developing ideas of the phylogeny, rather than in a step prior to a phylogenetic analysis. It is recommended that character states be delimited by carefully analyzed discontinuities (not necessarily absolute gaps) in the variation, attention having been paid to variation in the outgroup, and that "morphological" characters in general are assumed to be quantitative unless demonstrated otherwise. Explicit justification for the delimitation of character states should be given as a matter of course in all phylogenetic studies.

The goals of cladistic analyses are to infer phylogeny by explicit manipulation of data for the production of a cladogram, to provide a classification following phylogenetic principles, and to use the phylogeny to understand further evolution and biogeography. The first step is the selection of the study group; this should be monophyletic, and include monophyletic, or at worst paraphyletic, terminal taxa; hence, taxa of hybrid origin may pose problems. In lower-level studies all taxa are usually included, but in higher level studies a sample of taxa that includes the diversity in the major group may be included, each taxon being studied in detail (Hill and Camus 1986) or a summary of the knowledge of each taxon may be given (e.g., Bremer 1987) in which the sampling of each character is uneven. Characters are surveyed throughout the study group and its outgroup, the initial requirement being simply that each character can be recognized when it occurs in different taxa using criteria of similarity ("homology" of some: see Patterson 1982; Roth 1988; Stevens 1984). Characters are then divided into states, and these states polarized (Maddison et al. 1984 for references) and analyzed using one or a variety of algorithms in programs such as Hennig 86, MacClade, CAFCA, PAUP, and Phylip; analyses can of course be performed on unordered data. After trees are produced and evaluated, classifications based on those trees may be proposed; these classifications may follow the conventions proposed by Nelson (1979) and Wiley (1981).

Substantial progress has been made in most of these steps, but the step that has been analyzed least is that of subdivision of characters into character states, especially when the character is a quantitative variable. There is an implicit methodological assumption in phylogenetic analysis that character states are discrete (e.g., Pimentel and Riggins 1987), yet when reading lists of characters and character states, one all too often comes across states contrasted

by phrases like "calyx <5 mm long (0), calyx >5 mm long (1)," or "ray floret number <5.5 (1), 5.5–10.1 (0), >10.1 (2)." Recently, however, discussion about this most important step in phylogenetic analysis has begun (e.g., Almeida and Bisby 1984; Archie 1985; Baum 1988; Chappill 1989; Cranston and Humphries 1988; Goldman 1988; Pimentel and Riggins 1987; Thorpe 1984). Neff (1986) and Bryant (1989) have emphasized the complexity of the decision-making process at this stage, contrasting it with the subsequent analysis of character states. This paper broadens the scope of the discussion, although the issues raised are not easily resolved.

It is customary to distinguish between two kinds of quantitative characters. A "continuous quantitative character" is a character like leaf length in which individual measurements are not necessarily integers and potentially form a continuum, at least with the observational techniques adopted. A "discrete quantitative" ("meristic") character is one like petal number, in which any individual measurement is an integer; half petals generally do not exist. A "qualitative character" includes characters like xanthone type, where a plant may have a particular kind of chemical; calyx texture, in which observations may reduce to a particular quantity, e.g., amount of lignified tissue; and calyx thickness, in which an immediate quantitative basis is more evident. This classification of variation, although common (e.g., Abbott et al. 1985; Kendrick 1964; Nauman 1982; Sanderson and Donoghue 1989; cf. Smets and Crescens 1988; Stuessy 1990; van Welzen 1990), is of little help; although I focus on continuous and discrete quantitative characters, one of the main points I make is that many "qualitative" characters are phenomenologically quantitative. The distinction between characters and states that I draw is simply that of subdivision [the state(s)] of a series of measurements of a feature that are deemed to be comparable, or similar (the character). [In a phylogeny or cladogram the distinction between states is one of generality, or hierarchical level, e.g., Eldredge and Cracraft (1980) and Pimentel and Riggins (1987); Ghiselin (1984) distinguished between "parts" and "attributes," or called both, and "characters," simply "features." Stuessy (1990) provides a summary of the terms used.]

Below I outline the background to the problem of character state delimitation. I then analyze the literature to show how states have been delimited when variation is continuous and quantitative. I organize the analysis under the following sometimes rather ill-defined topics: 1) How states have been delimited when there is potentially continuous quantitative variation in the group whose phylogeny is under examination. 2) Additional complications caused by variation in the outgroup. 3) Whether "qualitative" variation poses problems that differ from those posed by quantitative variation. I then discuss ways of converting quantitative variation into character states and the broader implications of some of my findings. The examples come largely from published work; most phylogenetic studies using more than about 10 characters include at least one obviously quantitative character. As only studies of rather small genera or parts of genera are accompanied by basic data that show how character states were delimited, I use my own work on the Bonnetiaceae–Clusiaceae (the latter including the Hypericaceae)—a group of some 50 genera and 1640 species—to discuss the use of quantitative characters at higher taxonomic levels. Documentation of the variation encountered in higher-level analyses previously published (e.g., Bremer 1987; Burns-Balogh and Funk 1986; Kellogg and Campbell 1987) is too poor (but see below) to be useful in a review such as this. I conclude with a short general discussion and some suggestions as to how to deal with the problem of variation in quantitative characters in particular, and that of variation in general, in phylogenetic studies.

Background to the Problem

A brief digression is necessary to appreciate the dimensions of the general problem surrounding the delimitation of character states. J. S. L. Gilmour has been one of the most important figures in the development of higher-level systematic studies in this century, in large part because of the general compatability of his philosophy with that of phenetic taxonomy. Gilmour (e.g., 1940) emphasized the numerous ways in which the same sense (=observational) data could be classified; these sense data had an objective status, while classifications were simply convenient and subjective "clips" that held them together. Data then had an unquestionable ontological status; they were given once

and for all, and could not be altered. Classifications were either "special purpose" (for instance, they might reflect phylogeny) or they were of some maximum general utility. Phenetic taxonomy as it developed in the 1960's emphasized the deleterious effects of the selection and weighting of data by evolutionary taxonomists, emphasizing the importance both of gathering large amounts of data so as to minimize the effects of a taxonomist's bias, as well as of general purpose classifications (e.g., Sokal and Sneath 1963). A number of algorithms for analyzing these data were developed. From the phenograms produced, taxa could be circumscribed following consistent, if arbitrary guidelines (but see Michener and Sokal 1957). The emphasis remained on the manipulation of data rather than its critical initial evaluation: "Coding and scaling are steps that convert the crude data into a form suitable for computation and also preserve the kind of information the taxonomist wishes to consider in making a classification. . . . Many of the coding and scaling methods described above have not yet been thoroughly explored in practice" (Sneath and Sokal 1973, pp. 147, 153). Scaling was usually some form of mathematical transformation of data; coding, for Sokal and Sneath, included both the circumscription of states and how those states should be recorded, and they paid most attention to this latter aspect of coding in their very brief discussion of all these subjects. When dealing with how to code quantitative characters, Sneath and Sokal (1973) thought that the ideal procedure would be to recode them as several two-state characters since quantitative characters were likely to be controlled by more than one genetic factor. They thought it was, however, generally more practicable to recode them as two-state characters by dividing them arbitrarily.

There has been little subsequent discussion in the phenetic literature on how to circumscribe character states (e.g., Sokal 1986), although there are suggestions that imperfectly circumscribed states can cause problems (e.g., Burtt et al. 1970). As character states are not directly mapped onto most phenetic diagrams, the user of these diagrams cannot readily evaluate the relationship between data and product.

The focus of cladistic studies has remained on the manipulation of data, with extensive development of algorithms for data analysis. The nature of the data, of course, changed; groups have to be supported by particular kinds of character states, synapomorphies, and these synapomorphies are frequently displayed on the branching diagrams of relationships produced by cladistic analyses. However, character states themselves (and even characters, see Wiley 1981) have been treated as if they were primitive terms, with their definition (circumscription) rarely being discussed; Stuessy (1990) in his recent textbook barely touches on how to delimit character states.

This omission in the literature is my concern here. Several authors have realized that a problem existed in the delimitation of states when variation was quantitative. Thus, Stuessy (1979) was inclined to exclude obviously quantitative characters from his final analysis of *Melampodium* (Asteraceae) because of the high homoplasy that they showed, yet he used them to resolve the finer details of his phylogeny. LaDuke (1982, pp. 469–470) observed "Characters and character states are usually easily determined for qualitative characters and somewhat more difficultly for quantitative characters since character states are not usually evident"; he used few quantitative characters in his study. Judd (1984) worried about continuous variation and its somewhat arbitrary subdivision into states; he tried to delimit states so that as few taxa as possible showed two states, although not altogether successfully. Others have voiced similar concerns, e.g., Cantino (1982a), who excluded quantitative characters, and Campbell (1986), who included them. To Meacham (1984, p. 20) "The creation of a qualitative character is a complex operation that requires a great deal of biological interpretation and intuition . . . the process resembles an act of invention more than discovery." However, Meacham focussed on the issue of the polarity of character states, rather than on the rationale for the very existence of those states.

Almeida and Bisby (1984) suggested that character states should be absolutely discrete (not show overlap), or almost so, and showed that simple graphical techniques could be used to demonstrate the nature of any overlap between states. Archie (1985), on the other hand, delimited states in continuously-varying characters by using modified pooled averages of the standard deviations of the individual taxa; the number and circumscription of these states was

clearly an arbitrary matter. In fact, few authors, with the exception of Hennipman and Roos (1982; see also Hart 1985, in part), have provided evidence that the character states they are using are discrete. The opposing philosophies of Archie and of Almeida and Bisby still represent the extremes of the argument. Thus Baum (1988) advocated using continuous quantitative variation on the grounds that measurements that differ represented underlying genetic differences, and Thiele and Ladiges (1988) used such characters to increase the resolution of their cladistic analysis. On the other hand, Pimentel and Riggins (1987) and Cranston and Humphries (1988) rejected the use of continuous data in cladistic analysis. As the latter authors observed "[M]ost quantitative data are not discontinuous, but represent series of overlapping values. In these cases, as performed at length on some characters in this study, means must be calculated and statistical tests applied to group those means into meaningful subsets. But, then what is the cladistic significance of a mean for a taxon? . . . For these reasons, we feel that continuous data are best excluded from analysis" (Cranston and Humphries 1988, p. 81).

It will become clear that the subdivision of many quantitative characters into character states is arbitrary, and other circumscriptions of the states would have been as defensible as those actually adopted. The problem with such characters is exacerbated by the fact that much qualitative variation has a quantitative basis; such characters are only semantically qualitative (Stevens 1987). As will be shown, most of the "qualitative" characters of authors such as Chappill (1989), Duncan (1980b), and Estabrook and Anderson (1978) are of this kind. All analyses, phylogenetic or otherwise, are constrained by the initial circumscription of character states. As Bisby and Nicholls (1977, p. 104) noted, "what angiosperm taxonomists would think of as small changes in character formulation can lead to large differences in the taximetric classification within the Genisteae." Many of the characters that Bisby and Nichols included in their study were basically quantitative, although apparently qualitative.

Felsenstein (1988a, p. 462; see also 1988b) in his survey of the problem of obtaining phylogenies from quantitative characters, a survey which focussed more on the level of population and gene, concluded ". . . I am skeptical of all schemes for discrete character coding [of quantitative variables]. There is no requirement that phylogenies be based purely on data with discrete states. None of the authors on coding methods has yet faced the questions of how we could test for the presence of underlying discrete states. Lacking such a test, there is no reason to discretize quantitative characters. The real 'character coding problem' is that people insist on discretely coding quantitative characters that would better be left on continuous scales."

Even leaving aside Felsenstein's argument for the time being, since many morphological characters are fundamentally quantitative, and such characters present problems, we are in serious trouble. Most phylogenetic studies using morphological data make a methodological assumption that character states are discrete. We have created discrete character states as much or more for methodological as for biological reasons (see also Roth 1991), a point to which I shall return.

Quantitative Characters and Variation—The Basic Problem

In this section I present graphs depicting variation in quantitative characters as provided by descriptions in published literature, and show how this variation has been divided into states. The bar graphs have been arranged so that the measurements of the character as given in the treatments discussed are on the ordinate, while individual taxa are arranged along the abscissa in order of increasing midpoints (or means, when available) for that character. The number of bars (taxa) in graphs dealing with the same study may differ if data for a character were not given for all taxa. Where relevant, I try to place the character in the context of the whole study, e.g., is one (or more) of its states a synapomorphy for a major clade, or does it show very high homoplasy?

It is important to note that neither characters nor studies have been specially selected. The studies encompass a variety of families, although the Asteraceae inevitably preponderate. All studies that I have examined are mentioned below; none is excluded. I analyzed all quantitative characters for which there were basic data, with exceptions such as Campbell (1986), Duncan (1980b), Estabrook and Anderson (1978),

and Gardner and LaDuke (1978) where quantitative characters are in the majority; here I looked only at a selection of characters from different organs. I have largely ignored autapomorphies as they provide no information about relationships between terminal taxa, but even they are not exempt from the problems discussed below. The nomenclature used follows that of the authors cited, but I have converted all the scoring to ordinal, where 0 is the plesiomorphic state and the others apomorphic. Additional examples are provided in the Appendix, but reference in the text is made, where relevant, to figures in the Appendix.

Quantitative Characters. INGROUP VARIATION. Here I illustrate the delimitation of continuous quantitative characters in the context of ingroup variation. In the majority of cases the basic variation is clearly more or less continuous, even though the states have been treated as if they were discrete.

In a study of relationships in the Scrophulariaceae–Maurandyinae (Elisens 1985; fig. **1A**), the only overtly quantitative character used was the degree of connation of calyx segments, the states being free or connate <¼ of the segment length (0), and connate for ⅓–⅔ of the segment length (1). The variation in this character is more or less continuous and alternative subdivisions of the character are clearly possible. The derived character state as delimited by Elisens provides a substantial amount of structure to the cladogram. Redefining the states as no fusion vs. some fusion would make the circumscription of *Mabrya* problematical; simply rescoring *Mabrya geniculata* would decrease the homoplasy of the cladogram, but the basic circumscription of states would remain questionable.

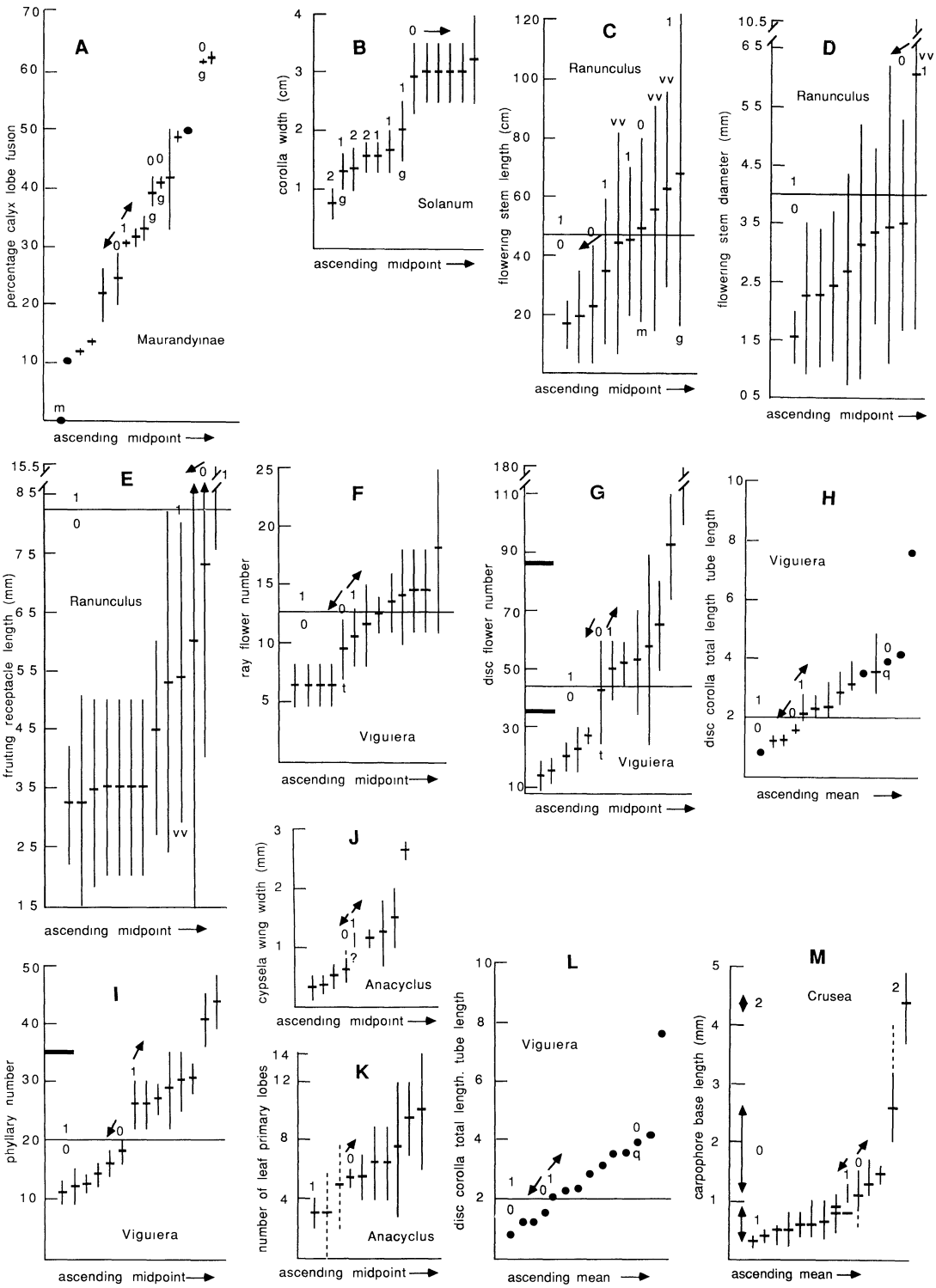
Corolla size (width measurements alone were given) in *Solanum* sect. *Androceras* (Solanaceae) was divided by Whalen (1979; fig. **1B**) into three states, small (2), medium (1), and large (0). The first two states are not clearly separated, and there is slight overlap even if only two states, large vs. small, are recognized. In Whalen's phylogeny, the character state "small corolla" arose three times, but the basic structure of the cladogram is shaky and rescoring of states causes topological changes.

The characters used in a phylogenetic analysis of the *Ranunculus hispidus* complex (Ranunculaceae; Duncan 1980b; data from Duncan 1980a; fig. **1C-E**) were described as being qualitative, with each taxon having but a single state; there are in fact eight continuous quantitative characters, and one discrete quantitative character. The variation in three of these eight characters (the others were ratios, a class of characters that has problems apart from simple continuity; see Pimentel and Riggins 1987) shows more or less overlapping character states (fig. **1C-E**). Overlap was relatively slight in two characters, the diameter of the flowering stem and the length of the receptacle at fruiting, but much greater in the character of the length of the flowering stem where infraspecific variation in two species, *R. macranthus* and *R. geranioides*, spanned both states.

Variation in five quantitative characters used by Panero and Schilling (1988; fig. **1F-I, L**) in their study of *Viguiera* sect. *Maculatae* (Asteraceae) was analyzed; note that these authors ordered data by ascending means. In three of these characters, ligule length, phyllary number (fig. **1I**), and ray flower number (fig. **1F**) states are clearly delimited at places where there are distinct or almost distinct break-points in the data, i.e., there was no overlapping variation. Overlap between the two states recognized in the character of ligule length [10–25 mm (0), 26–43 mm (1)] is caused by the imperfectly known *V. sharpii*. Additional states are perhaps recognizable in the characters of phyllary number (fig. **1I**) and disc flower number (fig. **1G**), and in the latter the position of *V. trachyphylla* is ambiguous. *Viguiera trachyphylla* is also uneasily placed in the character of ray flower number (fig. **1F**), and alternative circumscriptions of the states are possible. The apomorphic states of two of these characters, ray flower number and phyllary number, are the only synapomorphies for one of the basal clades of the section.

It is unlikely that ordering by means would resolve overlap in state delimitation evident in these graphs. Thanks to the kindness of J. L. Panero both means and ranges for another character, the ratio of the disc corolla length : tube length (properly throat length : tube length, Panero, pers. comm.) are given. Two character states can perhaps be separated, but if ranges had not been included, separation into states would have been impossible using simple gap coding (cf. fig. **1H, L**: the scoring of *V. quinqueradiata* is apparently a mistake).

From work on *Anacyclus* (Asteraceae; Humphries 1979; see Humphries 1983 for corrected


A
percentage calyx lobe fusion
Maurandyinae
ascending midpoint
B
corolla width (cm)
Solanum
ascending midpoint
C
Ranunculus
flowering stem length (cm)
ascending midpoint
D
Ranunculus
flowering stem diameter (mm)
ascending midpoint
E
Ranunculus
fruiting receptacle length (mm)
ascending midpoint
F
ray flower number
Viguiera
ascending midpoint
G
disc flower number
Viguiera
ascending midpoint
H
Viguiera
disc corolla total length tube length
ascending mean
I
phyllary number
Viguiera
ascending midpoint
J
cypsela wing width (mm)
Anacyclus
ascending midpoint
K
number of leaf primary lobes
Anacyclus
ascending midpoint
L
Viguiera
disc corolla total length. tube length
ascending mean
M
Crusea
carpophore base length (mm)
ascending mean

scoring and cladogram; fig. **1J-K**) I have analyzed variation in two characters. In the character width of cypsela wing there is an indistinct break between narrow (0) vs. broad (1) wings, a break made somewhat problematical by uncertainty in the lower value for wing width of *A. clavatus* (fig. **1J**). In that of number of basal leaf divisions or primary lobes the two states are many (0) and few (1), and there is a break with only slight overlap; the greater overlap caused by my inclusion of the number of divisions of the rosette leaves can be ignored because rosette leaves and basal leaves are not strictly comparable (fig. **1K**), an issue to which I shall return.

Anderson (1972; see also Estabrook and Anderson 1978; fig. **1M**, Appendix, fig. **5A-E**) considered the "raw data" to be represented by the means of each character (cf. Archie 1985; a similar approach is advocated by Prance and White 1988). Character states are then described in a way that suggests that there are gaps between them, thus the three states of carpophore base length are given as 0.3–0.9 mm, 1.1–2.6 mm, and 4.4 mm. These states simply span the means of the taxa included in them, but they do not necessarily translate to gaps even when means alone are considered (see fig. **1M**). Duncan (1980a) similarly converted quantitative into qualitative characters by designating breaks in histograms of mean values (ranges are converted into points) and as the boundaries of the states. As with *Viguiera*, gaps evident when means alone are compared are obscured when ranges are included.

Moran (1987; fig. **2A-B**) divided lamina length in *Polybotrya* (Dryopteridaceae) into two states; there is both unclear separation of states and erratic assignment of states to taxa. Spore length was also divided into two states, albeit with extensive overlap (fig. **2B**). However, Moran (pers. comm.) recognized the two states so as to separate the sister taxa *P. sorbifolia* and *P. fractiserialis* alone, although he scored the character for the whole genus (see also below).

Roos (1985; fig. **2H-K**) used numerous quantitative characters in his study of the Drynarioideae. His rationale for the separation of states was as follows: "Characters with a continuous range are arbitrarily divided into separate states so as to represent optimally the observed discontinuities within the group. In case of characters with a meristic range, each value is usually treated as a separate state. Sometimes, the combination of two values is regarded to represent a different character state.... Often, character states have been delimitated [sic] because of the extremes being distinct; confusing intermediates are scored for both extremes" (Roos 1985, p. 29). Again, although the extremes may be distinct when they are compared with each other, there are so many intermediates that obvious lines of demarcation between states are unclear. However, Roos is unusual in taking infraspecific variation into account in the scoring of the characters (see also Riggins 1987).

Looking at these examples, it is clear that, as Judd (1984) realized, the recognition of character states in quantitative characters is often apparently arbitrary. If there is no or little intrataxon variation, or the variation is not shown, with the graphs consisting of points rather than

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FIG. 1. For all diagrams, unless otherwise noted, variation is arranged following increasing means or midpoints. Vertical bars = ranges; dots = measurements for which no variation is given, or for which the scale of the diagram renders depiction of variation impossible; dashed lines = extreme variation; horizontal bars = means or midpoints, as appropriate; upwardly pointing arrows = variation described in phrases like "up to 2 m in length"; arrows terminating lines at the top of the graph = variation greater than can be accommodated in the graph; question marks = uncertainty about measurements; horizontal lines right across the diagram = limits of states (when these are described); coding for these states is indicated by numbers close to the lines; states of individual taxa are denoted by numbers immediately above individual bars or dots; an arrow associated with these numbers means that all taxa in the direction of the arrow have the same state unless otherwise indicated. Data taken from publications cited in the text. Additional explanations are as follows: A. g, varieties of *Mabrya geniculata*; m, several species have free sepals. B. g, varieties of *Solanum grayi*. C–E. vv, taxa with varieties, some of which were scored separately as 0, others 1; data were given for the species only. C. m, *Ranunculus macranthus*; g, *R. geranioides*. E. Midpoint for the taxon on the right is 11.55. F, G. t, *Viguiera trachyphylla*. G, I. Heavy horizontal bars, possible additional states. H, L. q, *V. quinqueradiata*. K. Dashed vertical lines are measurements taken from rosette leaves. M. Double-headed arrows close to ordinate, character states as described by Estabrook and Anderson (1978).

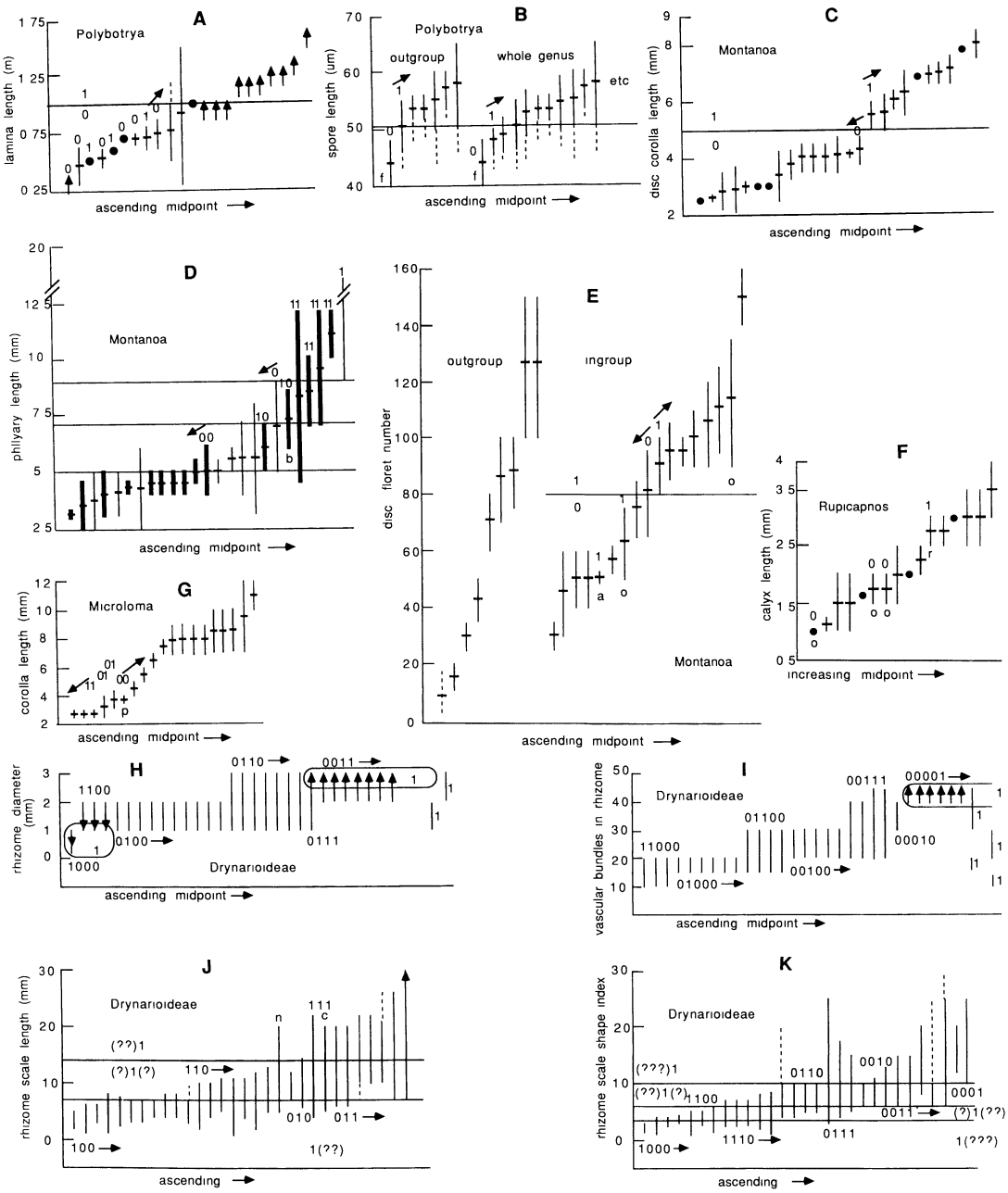

FIG. 2. See caption to figure 1. B. f, *Polybotrya fractiserialis*; outgroup, variation of *P. fractiserialis* in context of its immediate outgroups; whole genus, variation in the context of the genus as a whole. D. Heavy vertical bars, ingroup taxa (subg. *Acanthocarphae*); light bars, outgroup taxa (subg. *Montanoa*); b, *Montanoa bipinnatifida*. E. o, varieties of *M. ovalifolia*; a, *M. angulata*. F. Variation in *Rupicapnos longipes* ssp. *reboudiana* (r) and its immediate outgroups (o); bars without states represent the other taxa in the genus. G. p, *Microloma poicilanthum*. J, K. Taxa grouped following their assignation into character states, character state coding follows Roos (1985; see for further details). J. c, n, *Aglaomorpha coronans* and *A. novoguineensis*.

bars, the problem becomes even worse; simple comparison of mean values to detect gaps is a problematic operation. The issue of scaling the variation, for example, plotting it logarithmically or semilogarithmically, has rarely been considered (but see Chappill 1989; Thiele and Ladiges 1988); such plots will affect what is perceived to be a gap. In most examples examined here, taxa with variation straddling two states were scored as possessing only one of those states. Finally, although some authors explicitly ranked variation in terms of ranges and means, it is often unclear how such ranking was carried out. However, ranking by means, rather than midpoints, is no solution to the general problem of overlapping variation; the ordering of taxa may change, but the overlap will not go away.

VARIATION IN THE OUTGROUP. Variation in the outgroup and how it affects delimitation of states in the ingroup is a difficult topic to discuss because details of the former variation are rarely given. When analyzing the consequences of this variation on both the delimitation and the polarity of states in the ingroup, I follow the general procedure recommended by Maddison et al. (1984). The basic problem is whether character states as delimited in the ingroup are the same in the outgroup. This discussion applies also to those studies in which quantitative characters have been used to evaluate relationships of only part of the ingroup; the variation in that part can be compared with that of the rest, which forms a functional outgroup (see Watrous and Wheeler 1981).

Funk (1982; fig. **2C-E**) added characters to analyses of subgroups that were unresolved in an initial analysis of *Montanoa* (Asteraceae); these characters could not be used in the initial analysis because they were not divisible into states at that level. One quantitative character that was used in the analysis of subg. *Montanoa*, the length of the corollas of the disc flowers, showed non-overlapping states (fig. **2C**). Unfortunately, variation in the genus as a whole cannot be ignored even in the subanalyses, as the functional outgroup of *Montanoa* subg. *Montanoa* is subg. *Acanthocarphae*, and vice versa—the two are sister taxa. Thus, two states of the character phyllary length [5–9 mm (0) vs. 9–18 mm (1)] were recognized in the analysis of subg. *Montanoa*. Two more characters based on phyllary length were recognized in the subanalysis of subg. *Acanthocarphae;* these were phyllary length [1–5 mm (0) vs. 5–7 mm (1); and 5–7 mm (0) vs. >7 mm (1) (fig. **2D**)]. Division of these characters into states is perhaps questionable, even in the context of variation in the ingroup. *Montanoa bipinnatifida* is uneasily placed for it has phyllaries 5.2–5.7 mm long, yet it is scored as having the plesiomorphic condition. Character states taken from variation in phyllary length provided much cladistic structure for the *M. laskowskii* supergroup.

From the cladistic structure in the outgroup (subg. *Montanoa*) provided by Funk, the variation in phyllary length can in fact be analyzed further, and the basal condition in the outgroup may be around 2.5–6 mm, rather than 2.5–18 mm, the total range in the outgroup. However, to obtain such results, one needs a more or less resolved phylogeny of the sister group, not simply a knowledge of what the sister group is.

Another character used in subdividing the *M. laskowskii* supergroup is the number of disc florets, which is divided into two states (fig. **2E**). Again, if the variation in the outgroup is compared *in toto* with that in the ingroup, no support is offered to the subdivision of the character in the latter. However, if the cladistic structure in the outgroup is taken into account, the basal state may be less than 50 florets (the total variation in the outgroup is 3–150 florets).

There are a number of examples where evaluating the variation pattern within a subgroup allows detection of states the existence of which were not evident in an analysis of variation in the group as a whole. Sanders (1981; for data see Sanders 1987) added characters for fine resolution of phylogenetic structure. These characters varied both within *Agastache* sect. *Agastache* (Lamiaceae) and the tribe Nepeteae, in which it is included, and so could not be used in the initial analysis, but they were consistent within species groups of sect. *Brittoniastrum*. Thus the *A. wrightii* group was subdivided using corolla size; the sister group to this group is the rest of sect. *Brittoniastrum*. Ignoring variation outside this section, the variation within it can be represented as follows: [((*micrantha*—3–4.4 mm) (*wrightii*—4.5–6.5 mm)) (rest of section—7–40 mm)]. There are in fact non-overlapping states recognizable at the sectional level, but whose polarity becomes clearer only when there is some further cladistic structure. Calyx size, short (0) vs. long (1), differentiates between the

subspecies of *Rupicapnos longipes* (Fumariaceae; Lidén 1986; fig. **2F**). Looking at variation in the immediate outgroup of *R. longipes*, this subdivision may be reasonable, but in the genus as a whole the only gap in the variation is at the 2.5 mm mark, since long calyces also occur in the subspecies of *R. africana* [states of another character, flower size (small vs. large), were delimited by a gap in the variation in the genus as a whole]. Similarly, character states for corolla length in *Microloma* (Asclepiadaceae; Wanntorp 1988; fig. **2G**) are clearer in the context of variation in the immediate outgroup. *Microloma poicilanthum* is cladistically unrelated to other taxa with small corollas and its corolla size is apparently scored following its relationships. Moran (pers. comm.) explicitly compared species of *Polybotrya* in the context of a developing phylogenetic hypothesis when delimiting states in the character of spore length (see above; fig. **2B**). Here states are clearer when variation in only the two immediate outgroups is considered.

In the absence of cladistic structure, states may not be apparent. Stuessy (1979) used quantitative characters in *Melampodium* primarily to provide fine phylogenetic details, but states were recognized in the context of the variation of the whole genus. Outgroup variation was usually not discussed in detail; variation within the genus is continuous (see also Appendix, fig. **6B-D**).

Meerow (1987; fig. **3A-C**) discussed variation in the outgroups when evaluating the polarity of the characters in the ingroup, *Eucrosia* (Amaryllidaceae). Four characters, petiole length, flower number, pollen diameter, and amount by which the stamens were declinate, had a "polymorphic" state in one or more of the outgroups, but not in the ingroup. The polymorphic state, in which variation in the taxon transgressed the boundaries between the other states, was not treated as part of a transformation series, but as an apomorphy derived independently from the plesiomorphic state. If it is treated as part of a transformation series, or as a polymorphism, the polarities may differ.

In the character of flower number, the two immediate outgroups were polymorphic. *Both* states of the ingroup are derived if the intermediate is treated as part of a transformation series (fig. **3A**). In pollen diameter the second outgroup was polymorphic (fig. **3B**); polarity of the ingroup states was again unambiguous. In two other cases, petiole length and amount by which the stamens were declinate, only one member of the first outgroup was polymorphic, and there was no effect on the polarity of the ingroup states however intermediacy was interpreted (fig. **3C**), although if both members of the first outgroup had been intermediate, polarity of the ingroup would become ambiguous.

To summarize, outgroup variation has two main effects on the phylogenetic implications of variation of quantitative characters in the ingroup. The first, which is not a problem of quantitative characters alone, is that the assignment of polarities is often questionable when outgroup variation is ignored, even if it is assumed that the ingroup states are discrete; Thiele and Ladiges (1988) and Chappill (1989) both found problems in polarizing the states of quantitative characters because of outgroup variation. The basal conditions of quantitative characters in outgroups are rarely known. The second problem is connected to the first. Variation in the outgroup may straddle two states that are discrete in the context of the ingroup. If outgroup phylogeny is resolved, the condition at the base of these outgroups may become evident, but simply knowing the identity of the outgroup and the variation it contains is not enough. If ingroup variation is both continuous and more extensive than outgroup variation, it cannot be assumed that the bounds of outgroup variation necessarily delimit states in the ingroup.

Qualitative Variation. Much of the information presented in species descriptions, or discussed in the separation of closely related genera, has already been "processed" into character states and seems to represent qualitative variation. However, if such qualitative variation is examined carefully, it will be found that much describes an underlying continuum that has been transformed by the terms we use; discontinuities are only semantic (Felsenstein 1988b; Hart 1985; Stevens 1987). Hence, suggestions that qualitative and quantitative variation characterize different levels of the taxonomic hierarchy (e.g., Ashton 1982) are problematic. Indeed, a belief that there are two kinds of variations is widespread; R. W. Sanders (pers. comm.) noted that, at a symposium on "The concept of the genus" at the A.I.B.S. meetings

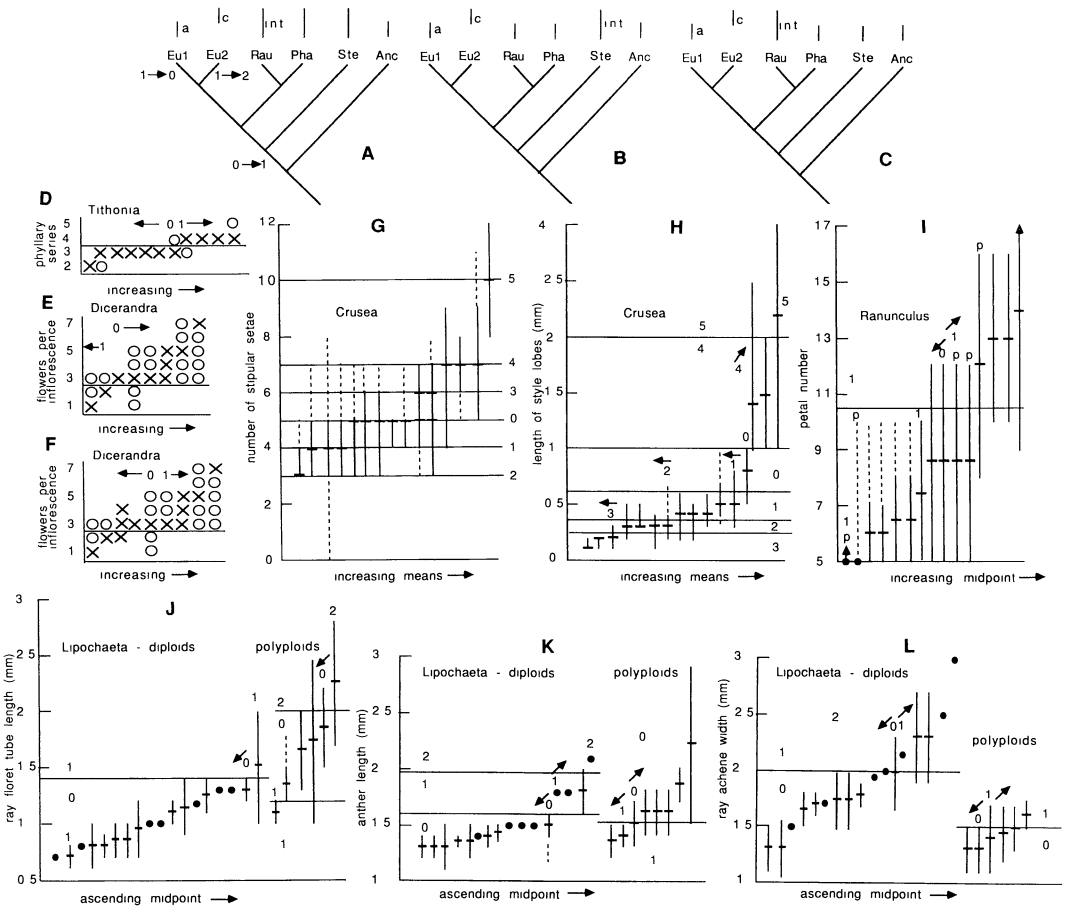

FIG. 3. See caption to figure 1. A–C. Variation in the outroups of *Eucrosia*. Eu1, Eu2, subgroups of *Eucrosia*; Rau, *Rauhia*; Pha, *Phaendrassa*; Ste, *Stenomesson*; Anc., ancestor. A. State changes assuming the intermediate is part of a transformation series (pattern similar if it is polymorphic). D–F. X, normal variation; O, exceptional variants. I. p, varieties of *Ranunculus petiolaris*.

in 1987, "most, perhaps all, of the speakers . . . maintained that the two types [quantitative and qualitative variation] are different in essence."

Standardization of the terms used to describe plant parts has long been important in botany, and was part of Linnaeus' reform of the discipline of taxonomy (e.g., Stafleu 1971). His immediate successors continued the process, focusing on particular ambiguities such as the Linnaean term "nectary" (see Schmid 1988 for references). Important subsequent attempts to standardize terms include those of A.-P. de Candolle (e.g., 1819), Lindley (1841), Gray (1879), and Stearn (1983). Particular organ systems have their own standardized terms, for example, plant architecture (Hallé et al. 1979), leaf architecture (Hickey 1979), pollen (e.g., Erdtman 1971; cf. Blackmore and Barnes 1987), and wood anatomy (Wheeler et al. 1989). In addition, large groups such as the Asteraceae, Poaceae, and Orchidaceae have their own terms.

Botanical terms are often not based on the evolutionary origin of structures, or even on their developmental origin, but simply on their superficial appearance; some terms may nevertheless imply very particular evolutionary or developmental origins (e.g., Sattler 1978). Use of such terms is stabilized by convention, a convention that is all-too-frequently associated with their reification. Thus, features like the shape of the stem in transverse section, the apex of the leaf, and the development of a border to

the pits of fibres, all have a particular set of terms used to describe them. However, there is no necessarily sharp distinction between alate or terete stems, between acuminate and retuse leaf apices, or between minutely-bordered fiber pits (a libriform fiber) and distinctly-bordered pits (a fiber tracheid). As is noted in Wheeler et al. (1989, p. 221), "Although there is more discrete diversity in wood structure than many other plant parts, there is also much continuous variation, and any attempt to classify this diversity into well-defined features has an artificial element." Similar problems face many terms used to describe spore (pollen) surfaces, and features of venation such as eucamptodromy and brochidodromy. Levin (e.g., 1986a, 1986b) was encouraged to use foliar characters in a phylogenetic study of the Euphorbiaceae–Phyllanthoideae because "a precise and non-overlapping" terminology for the description of dicotyledonous leaf architecture (Levin 1986a, p. 73) had been developed. However, that the terminology is non-overlapping does not translate to the existence of discrete states.

Furthermore, many characters that are described as being either present or absent may actually represent quantitative variation. When is winging of a stem, an auricle at the bottom of a leaf, or a glaucous covering on the underside of a leaf, *really* absent? At the phenomenological level at which most of us work, the decision may well be arbitrary. Thus, although 12 of the 48 characters used by Humphries (1979) in his study of *Anacyclus* are described as presence-absence characters, most do not have to be so divided. Membership in this class is very susceptible to semantic adjustments.

All too many morphological and anatomical characters used in botanical phylogenetic studies, even those in which attempts have been made to exclude quantitative characters, are quantitative. As quantitative characters they face the problem of more or less arbitrary subdivision of a continuum of variation that is discussed above. This is clear when reading descriptions of the variation shown by these characters, or looking at illustrations that depict features like pollen or seed surfaces. Goldblatt (1987) described the exsertion of the ovary from the spathe in the six species of *Hexaglottis* (Iridaceae) he examined as follows: exserted (two species)/usually partly to entirely exserted/just exserted/apex often exserted/included. The latter two conditions were considered to represent the derived state. Similarly, Stuessy (1979) subdivided phyllary connation in *Melampodium* into two states, separate or slightly connate (0) and connate ⅙–¾ their length (1). *Melampodium rosei*, with phyllaries connate for ¼ or less, is scored as being plesiomorphic, but in general the distinction between ⅙ connate and "slightly connate," the condition for the majority of species (Stuessy 1972), must be difficult to make (see also Elisens 1985; Simpson 1989; Todzia 1988). Characters such as leaf attachment (sessile or subsessile vs. petiolate) and outer phyllary margin (herbaceous vs. scarious), face the same problem.

Jansen (1985) subdivided variation in the shape of the outer phyllaries in *Acmella* (Asteraceae) into two states, broadly ovate (0) and linear to lanceolate (1). The descriptions in Jansen's treatment gave the following series of phyllary shapes: linear-lanceolate/lanceolate/lanceolate to narrowly ovate/lanceolate to ovate/lanceolate to broadly ovate. The apomorphic state included the first three conditions listed above, although *A. leucantha* and *A. calva*, described as having lanceolate to narrowly ovate phyllaries, were assigned to plesiomorphic condition. Along similar lines, Humphries (1979) distinguished between obovate and lanceolate receptacular scales, the latter condition being derived. Of the three species scored as having this state, only one (*Anacyclus linearilobus*) is actually described as having lanceolate receptacular scales, those of the other two are described as being obovate-acuminate (*A. nigellifolius*) and obtrullate to narrowly obovate (*A. latealatus*). The other species are described as having obovate, obcuneate, cuneate, or oblong (or some combination of these shapes) receptacular scales. Another character dealt with inflation of the peduncle, the two states being unthickened along its length (0) vs. thickened (1). This character suffers from similar problems, and Humphries (1979, 1983) wisely omitted it from his analysis. Illustrations provide examples of similar problems, as in the surface of the seed in *Solanum* (Whalen 1979), the shape of the median lobe of the corolla in *Agastache* sect. *Agastache* (Sanders 1981), and receptacle shape in *Ranunculus* (Duncan 1980a).

Aside from such "qualitative" characters, there is no clear distinction between meristic and continuous quantitative characters. Jansen (1985)

found no infrataxon variation in the number of series of phyllaries on the capitulum in *Acmella*; states were clear-cut. LaDuke (1982; fig. **3D**) recognized two states in this character in *Tithonia* (Asteraceae); there is some variation here. As the numbers of units in such characters increase, the variation pattern approaches that of continuous quantitative characters. This is evident in the number of flowers per inflorescence in *Dicerandra* (Lamiaceae; Huck 1987). One taxon was later added and the states delimited differently (Huck et al. 1989; cf. fig. **3E, F**), but it remains difficult to see character states. Other examples are petal number in *Ranunculus* (fig. **3I**; Duncan 1980b) and number of stipular setae in *Crusea* (Rubiaceae; fig. **3G**; Estabrook and Anderson 1978). Variation in the latter character is similar to that in a continuous quantitative character, length of style lobes (cf. fig. **3H**), in which rounded means alone were considered when delimiting character states (see also fig. **2I**: Drynarioideae).

Some authors have suggested that all the characters they have used in their studies are qualitative (e.g., Estabrook and Anderson 1978; Duncan 1980b), although many of the character states they recognize represent overlapping ranges of measurements. This is because the "non-overlapping" states are taken from an analysis of means of the variation and are separated by apparent gaps.

A final line of evidence bearing on the relationship between qualitative and quantitative variation comes from the data assembled in studies of allometric relationships in growth (e.g., Gould 1966, 1977 and references). What appear to be differences in shape ("qualitative") may be caused by variation in size ("quantitative"). Although much of this literature on allometry does not deal with character states, Gould (e.g., 1966) observes that a failure to understand the relationship between size and shape has caused taxonomists to emphasize variation in the latter when the former was what was varying.

The main point of this section is that many "qualitative" characters are apparently based on interpretations of continuous, quantitative variation. Both the way in which such quantitative variation is described, and the fact that quantitative and qualitative character states can often be interconverted by simple redescription, suggest that much so-called qualitative variation may not easily be represented by non-overlapping character states. There is a further problem with characters like color, where neurophysiological processes result in our seeing more or less discrete colors even though there are no forbidden wavelengths of light in nature.

Breaking More or Less Continuous Variation into States

There are various ways of converting continuous or discrete quantitative variation into states for phylogenetic studies. The two extreme approaches are to manipulate the variation so that discrete states appear, or to convert all differing measurements into separate states, on the grounds that they necessarily represent information that would be lost if they were to be combined in the same state.

A paper by Baum (1988) tends to this latter approach. Variation was ordered first by lowest measurement and then by midpoint; all taxa showing differences were placed in separate states and the character negatively weighted depending on the number of states it contained. If most taxa differ in either their midpoints or lowest measurements, numerous character states will be the result. In addition, there is no particular reason to adopt these criteria for ordering variation; even here decisions are being made as to what constitutes data. In table 1 various arrangements of the same taxa of *Kayea* (Clusiaceae) are compared; the different and decidedly non-congruent groupings of the same data result from choosing different criteria for ordering the variation. The choices are all defensible, and yet other ways of ordering the data will suggest themselves to the imaginative reader.

Baum (1988) suggested that phylogenies resulting from the analysis of highly subdivided quantitative variation can be evaluated by comparing them with common biogeographic patterns and with phylogenies proposed on other grounds. But, as with the other approaches just mentioned, the objection of "why were other criteria not used for grouping the variation?", can always be raised. There are the problems of simply fitting the data to a phylogeny (see below)—emerging biogeographic relationships may also affect the circumscription of states—or choosing between trees because one fits a

TABLE 1. Ranking of taxa of *Kayea* given different criteria for ordering the same data. Each letter in the alphabet represents a group of species that are identical given the ordering criteria employed; in the first column, the number of species in each smallest group is given. Note that if midpoints were replaced by means or modes, the compositions of the smallest groups would change (data from Stevens, in manuscript.).

Minimum + midpoint		Minimum	Midpoint and maximum		Midpoint
A-1	P-1	AB	A	P	A
B-1	Q-2	CDE	C	M	BC
C-3	R-1	FGHI	B	U	DF
D-2	S-1	JKLM	F	Q	EG
E-2	T-3	N	D	V	HJ
F-1	U-3	OPQRS	G	R	I
G-1	V-1	T	E	Y	KN
H-1	W-2	UVWX	J	W	LO
I-3	X-1	YZA'B'	H	S	MPT
J-5	Y-2	C'	I	Z	QU
K-2	Z-1		N	X	RV
L-1	A'-1		K	A'	SWY
M-1	B'-1		O	B'	XZ
N-2	C'-1		L	C'	A'
O-5			T		B'
					C'

common biogeographic pattern. Finally, Baum's approach strains the reliability of the data. Archie (1985) noted that raw data could simply be recoded following a rank order of taxon means for a particular character. He saw little to be gained by doing this, observing that the number (and ordering, it might be added) of the states would depend substantially on investigator error and precision of measurement (see also Clausen 1959 for comments on the reliability of such data).

Assuming different measurements are to be combined into states, one way to deal with variation is by restructuring the character and eliminating some of the measurements (1, below). Alternatively, intermediate measurements can be treated separately (2A), the hierarchical level at which the variation is analyzed can be changed (2B), or the whole pattern of variation can be reanalyzed (2C).

In general, consideration of the general variation pattern of a character in one particular taxon that seems to blur distinctions between otherwise discrete states may also be helpful; an understanding of the biological background to the variation is critical. When describing species, overlap in characters that are possible differentiae for those species does not necessarily destroy the case that the species can be separated using those very characters; when comparing characters in different taxa, subcontinuous variation does not necessarily immediately terminate the quest for sharply delimited character states.

1. Restructuring Characters. Problems with continuous variation may be pseudoproblems caused by how *characters* are circumscribed (see also Rasmussen 1983). In some cases measurements of what appear to be the same character on different organisms may be better treated belonging to different characters, or at least not to be directly comparable. A good example is that of the scoring of the number of divisions in the basal leaves of *Anacyclus* (Humphries 1979; fig. **1K**); variation of this feature in rosette leaves was ignored because such leaves were not considered to be comparable with basal leaves. Klackenberg (1985) provides a similar, although less clearly articulated, example in his character of calyx lobe fusion in *Exacum* (Gentianaceae), where fusion of calyx lobes was effectively being considered only in the context of calyx shape.

Other examples come from my studies in the Clusiaceae alliance. Only genera in the *Bonnetia* complex, *Archytaea* and *Ploiarium*, are scored as having serrate leaves (the polarity of this state is unclear), while the rest of the complex is scored as having entire leaves. This is despite the occurrence of more or less crenate leaves in *Hypericum* and *Psorospermum* in particular, and calyces with fimbriate margins in some species of the former genus. Such crenations and serrations nearly always occur in association with glands; if they are to be considered as a distinct character state this should be in the context of plants possessing latex glands. Similarly, there is no clear demarcation of different size classes of embryos when the embryos of all members of the group are considered together. However, rather large embryos occur in two quite distinct situations—when embryos are mostly hypocotylar and when they are mainly made up of much enlarged cotyledons. Despite the relatively few observations, it is difficult to distinguish character states of embryo size in taxa with large hypocotyls, but much easier in taxa with large cotyledons. Embryo size considered in the context of embryo type can provide information of potential phylogenetic interest; out

of this context, it cannot. This adds an important dimension to the whole problem; was the character correctly formulated in the first place?

2A. Separate Treatment of Intermediates. Pimentel and Riggins (1987) suggested that if both states occurred in a taxon, there was no justification for assigning that taxon to the plesiomorphic condition; they would seem to be correct. Taxa with the variable or intermediate condition might be scored as "missing data," as is sometimes done in higher-level cladistic analyses (e.g., Kellogg and Campbell 1987; Riggins and Farris 1983). Of course, the basic pattern of variation of the character should suggest that it can be divided into states.

Mickevich and Johnson (1976) adopted a different approach. They felt that simple presence/absence coding for allozyme data was more suitable than frequency coding, since acquisition of an allele, for cladistics, might be more important than subsequent modification of the frequency of that allele. Thus, if both states occurred, a taxon would be scored as having the derived state, regardless of its frequency.

Humphries (1979), on the other hand, scored taxa that showed either/or variation as having the plesiomorphic state. Thus *Anacyclus linearilobus*, despite having leaves that were described as "bi- to more rarely tripinnatisect," was scored as having the plesiomorphic condition (tripinnatisect). Similarly, *A. monanthos* sometimes had leaf rosettes, but was scored as lacking them (the plesiomorphic condition); it also lacked an associated condition, heteromorphic leaves. Scoring these three characters as apomorphies would increase homoplasy, but it would also be incorrect since the species are variable. Whatever course of action followed, variation and homoplasy are removed to another level of analysis. It could be argued that any homoplasy properly pertains to this other level, but decisions to score intermediate states as being apomorphic or plesiomorphic are still questionable.

Jansen (1985) dealt with variation in corolla merosity in *Acmella* by scoring the variable taxon as having a separate state: taxa were either 5-merous (0), 4- or 5-merous (1), or 4-merous (2); this approach was also favored by Zandee and Geesink (1987; see also van Welzen 1990). However, this weights positively characters in which there is an *incomplete* separation of states, for 4-merous taxa could then be united by two synapomorphies (this will depend in part on whether the character states are scored as ordered or unordered). If all taxa were *either* 4-merous *or* 5-merous, a simple two-state character would suffice and all 4-merous taxa would be united by but a single apomorphy. It might seem appropriate to assign less weight to the individual states of such multistate characters, but this is rarely done, as Cranston and Humphries (1988) note (but cf. Gowan 1990). However, as will become apparent, the theoretical basis for such weighting is shaky.

It might be argued that not recognizing the variation at all, i.e., scoring variable taxa as missing data, implies that there is no connection between taxa in which a character state is sometimes present and those in which it is always present. Cantino (1982b, 1985) and Felsenstein (1988b) have voiced similar concerns; variation may be connected to some sort of developmental potential, which is more fully expressed in some situations than others. Particularly at the supraspecific level, however, we see that there are various other ways in which variation can be treated that may allow such ideas to be discounted. Of course, it may be best to treat variation as a polymorphism, and Roth (1991) shows how this may affect the topologies of trees.

2B. Changing Hierarchical Levels. There are many examples in the literature of taxa that are apparently incorrectly scored. Although some cases are apparently simple errors, others are caused by the assignment of states to species rather than to the infraspecific taxa they contain. Examples of the problems this causes are found in *Solanum* (fig. **1B**; Whalen 1979), *Montanoa* (fig. **2E**; Funk 1982), *Melampodium* (fig. **6B-D**; Stuessy 1979) and *Andropogon* (Poaceae; fig. **7E**; Campbell 1986). On the other hand, the considerable variation within some species of *Agarista* (Ericaceae) is partitioned between infraspecific taxa that are scored appropriately (fig. **5K**; Judd 1984). Infrataxon variation can be appropriately handled when the ultimate taxa are treated as separate entities; the species as a whole can be assigned only a single state.

A similar problem was faced by Todzia (1988; fig. **4A**, see also Appendix), who found extreme infrataxon variation in her study of the phylogenetic relationships of species groups of *Hedyosmum* (Chloranthaceae). She used only characters that were "consistent" within the seven major groups recognized, except for three

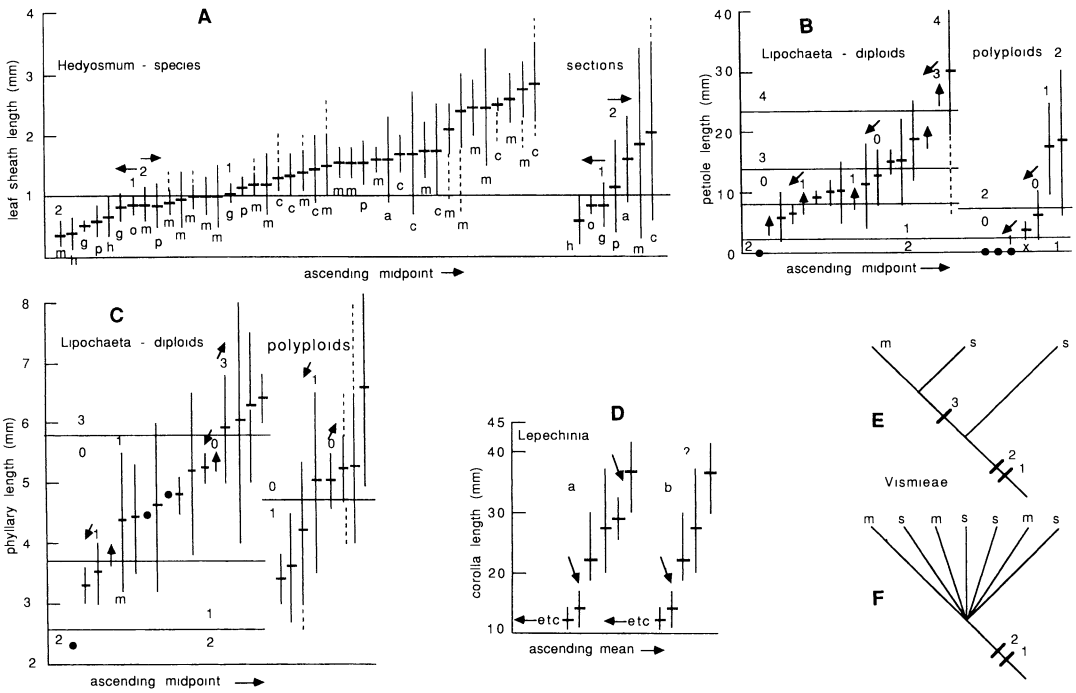

FIG. 4. See caption to figure 1. A. Analysis of variation at the level of species and of species groups; h, *Hedyosmum* group; o, *orientalis* group; g, *grisebachii* group; p, *pseudoandromeda* group; a, *artocarpoides* group; m, *microcarpa* group; c, *macrocarpa* group. B. x, the two varieties of *Lipochaeta lobata* are assigned different states, but petiole length is given only for the species as a whole. C. m, varieties of *L. micrantha* not described separately. D. Redrawn from Hart (1985, fig. 2, in part), inclined arrows, gaps between states; ?, questionable gap after removal of *Lepechinia speciosa*; etc, taxa with smaller corollas. E, F. Synapomorphies: 1, hairs on the adaxial surface of the petals; 2, indumentum of stellate hairs; 3, bracteoles in inflorescence displaced one internode. Terminal taxa are informal species groups.

characters (not mentioned below) over which there were caveats. However, the problem of continuity is as evident when the variation is analyzed with species or sections as the ultimate taxa. Here, even if states are referred to species or infraspecific taxa, and not to the species or other higher taxa that contain them, the basic problem of continuity remains.

Variation in subdivisible terminal taxa can sometimes be eliminated by making explicit phylogenetic hypotheses within the terminal taxa and situating the variation in the context of those hypotheses. This is an approach similar to that discussed earlier in the context of subanalyses of an only partly resolved phylogeny, but it is difficult to implement if the terminal taxa in the analysis are species, or groups of taxa whose phylogenetic relationships are unknown (Kellogg and Campbell 1987). It has been used by authors such as Bremer (1987) and Crisp and Weston (1988); Judd (1989) made an estimate of the ancestral condition when there was variation within terminal taxa. Donoghue (1983) scored taxa (groups of species) with more than one state as having the plesiomorphous state, unless this putatively plesiomorphous state occurred in a species that was otherwise highly derived. This argument is based on the correlation of characters (but cf. Stevens 1980) or on a local phylogenetic analysis (see below). Zandee and Geesink (1987, pp. 160–161) dealt with variation in an apparently rather similar fashion.

In the Clusiaceae alliance, it is possible to situate some species of *Vismia* and *Psorospermum* with relatively large embryos up to 6 mm long within the Vismieae if that group is used as a terminal taxon (fig. **4E**) and so ignore them in the division of the character of embryo size (or embryo type) into states. However, if an attempt

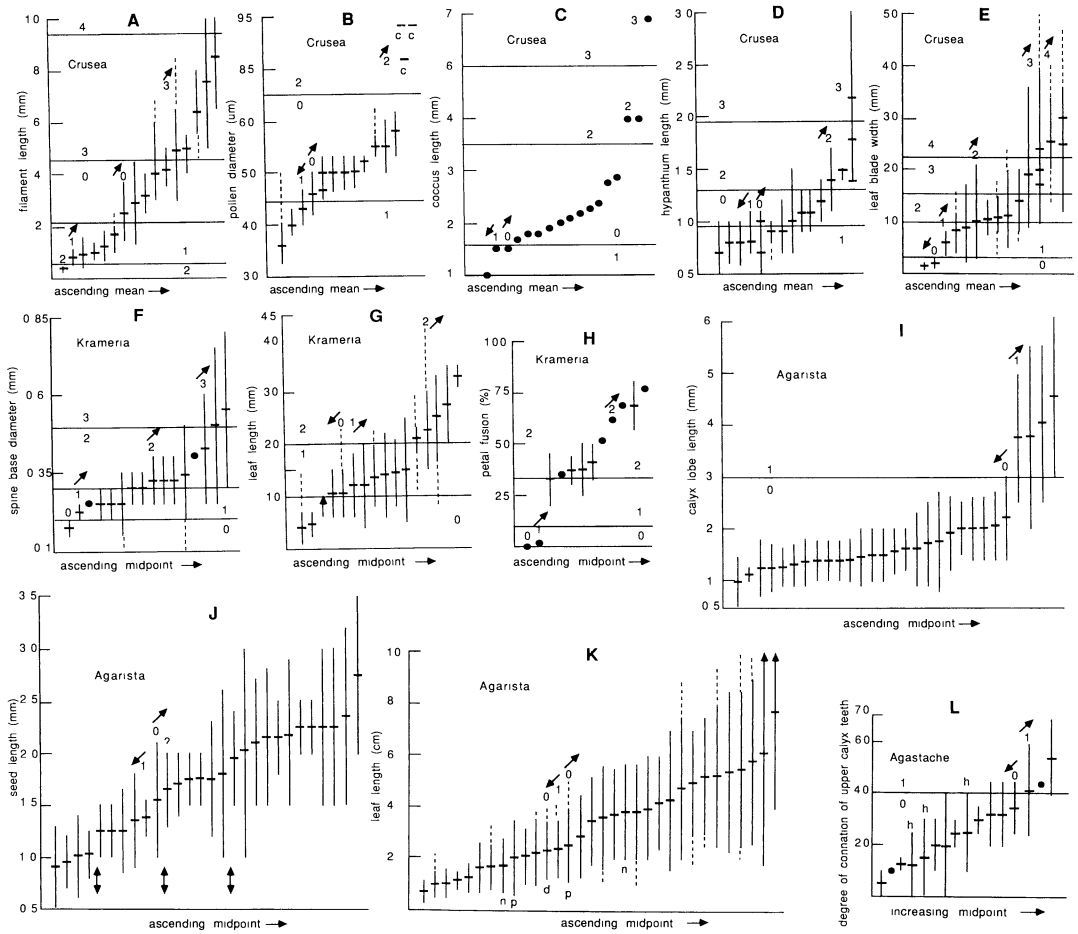

FIG. 5. See caption to figure 1. A. *Crusea hispida* var. *grandiflora* is the only taxon with character state 4; it has filaments 12–17 mm long. B. c, varieties of *C. coccinea*, means only given, not variation. D, E. Bars with more than one mean, means for varieties and variation for species as a whole. H. Several taxa have no petal fusion. J. ?, seeds of *A. subrotunda* are described as being probably also larger than measurements given. K. d, *Agarista duartei*; n, p, varieties of *A. niederleinii* and *A. pulchella*, respectively; double-headed arrows, possible additional states. L. h, hybrids.

is made to resolve the relationships within the various subunits of the Vismieae these embryos must taken into account in any basic division of variation into states (fig. **4F**). This is an important point to which I will return in the Discussion. Other variation in the Clusiaceae can be handled in a similar fashion. Thus, some species of *Calophyllum* such as *C. savannarum* have non-functional terminal buds, but this can be ignored in terms of scoring character states because it can be interpreted as being of independent origin. However, the poorly understood genera *Garcinia* and *Clusia* cannot be treated like this. In general, subdividing a terminal taxon in a cladistic study may be more effective if it shows meristic quantitative variation (Riggins and Farris 1983), but less effective with continuous quantitative characters.

A similar approach can be used when a variant occurs in only some individuals of one population of a species, or in one species in a genus, details of the relationship of population to species or species to genus being unknown. For the variant to indicate unambiguously the ancestral condition of the larger group, the taxon in which it occurs would have to be paraphyletic, with the variant being cladistically basal in the paraphyletic complex. If the taxon is monophyletic,

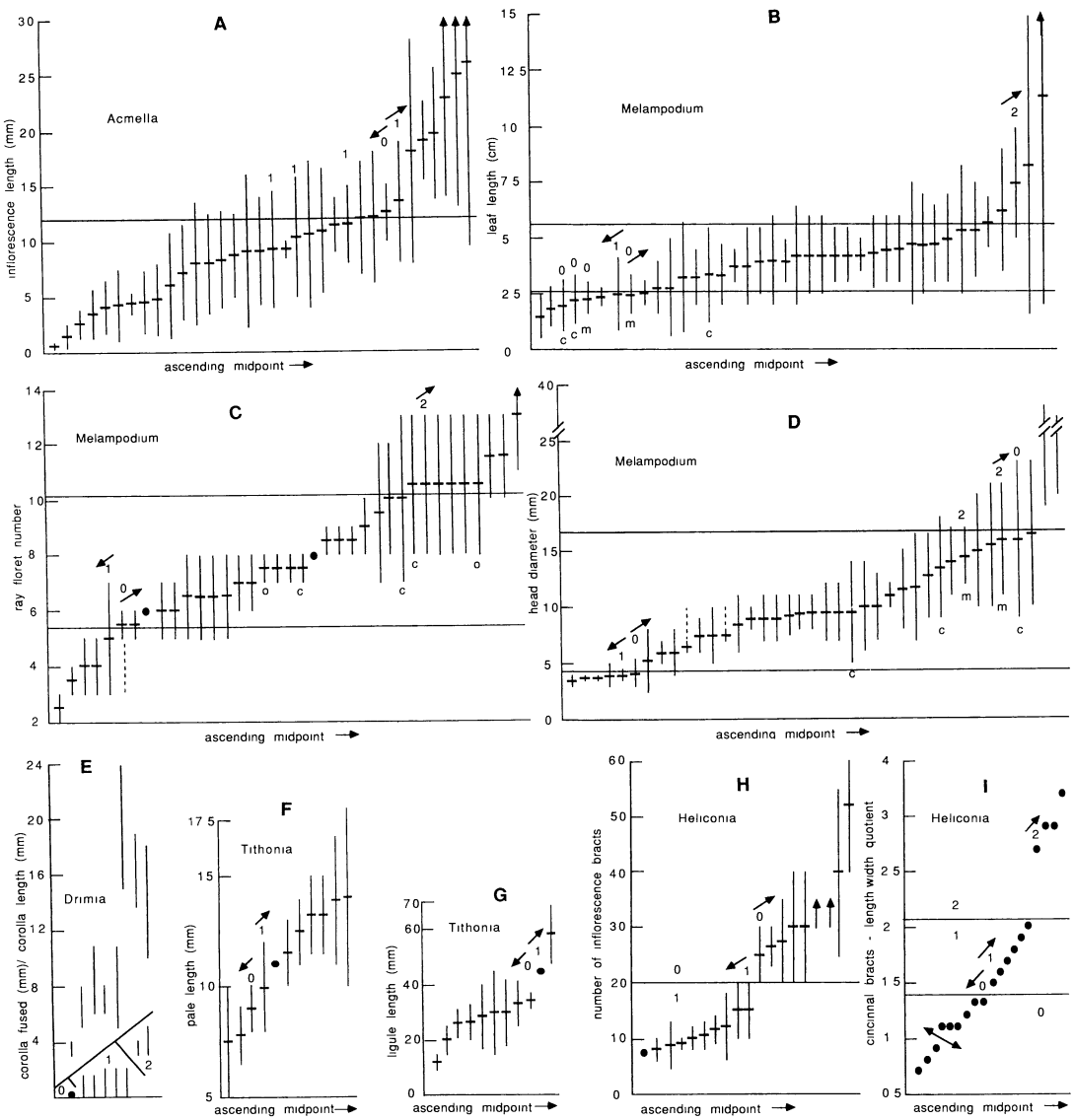

FIG. 6. See caption to figure 1. B, D. c, m, varieties of *Melampodium cinereum* and *M. montanum*, respectively. C. c, varieties of *M. cinereum*; o, some taxa with these values omitted from graph. E. Lines separate the character of corolla fusion (and its states as given by Stidje 1987) from corolla length. I. Double-headed arrow, possible additional states.

the phylogenetic importance of the variant will be at best equivocal. This argument has been used to eliminate rare states of a character that can be readily subdivided (e.g., Kellogg, pers. comm., in Kellogg and Campbell 1987), and it can be used to reduce the range of variation shown by a taxon prior to the decision to recognize states. Variation can sometimes be eliminated from consideration following the guidelines suggested by Frohlich (1987), which allow one to suggest the condition for the basal node of the ingroup in the absence of any detailed knowledge of ingroup phylogeny. In general, variants again represent homoplasies that will become evident only on finer resolution of phylogenetic relationships.

Akin to this approach is disregarding taxa that are of allopolyploid (hybrid) origin. Hy-

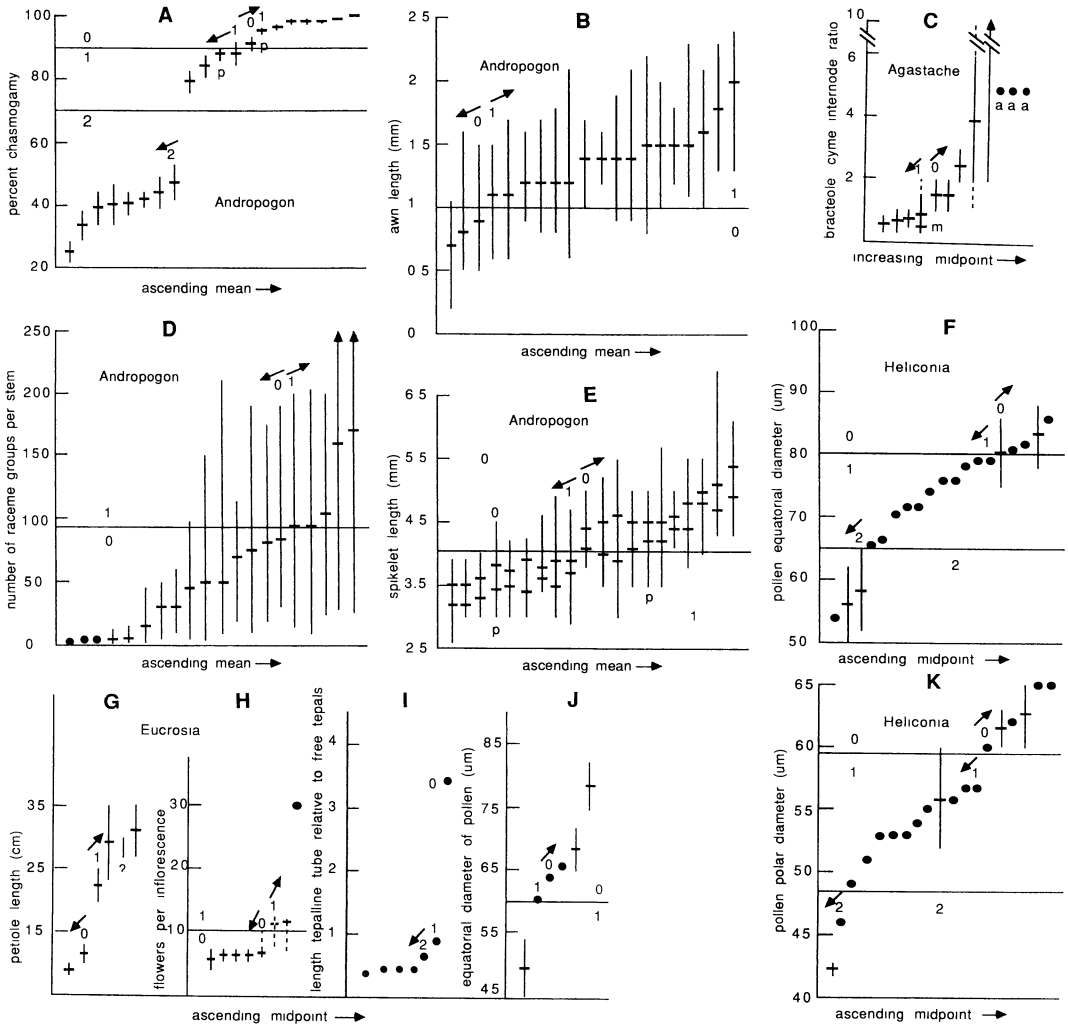

FIG. 7. See caption to figure 1. A. Vertical bars represent standard errors; p, variants of *Andropogon glomeratus* var. *pumilis*. C. a, taxa in which bracteoles are described as being much longer than the internodes of the cymes, m, modal value at bar, fide Sanders (pers. comm.). E. Lower and upper bars represent means of the smallest and largest values, respectively; p, variants of *A. glomeratus* var. *pumilus*.

brids may be excluded from phylogenetic analyses since they represent reticulation events. This may remove some variation that blurs boundaries between states, since hybrids tend to be intermediate. Thus, Gardner and LaDuke (1978) decided on character states in the diploid and polyploid species of *Lipochaeta* (Asteraceae) separately, although it does not help in the delimitation of discrete states in either group (figs. **3J-L**, **4B-C**). Sanders (pers. comm.) also removed hybrids when considering the delimitation of character states in *Agastache*.

2C. Reanalyzing Variation. Gap coding that is other than absolute, i.e., non-overlapping, may present ambiguities. Thus, Hart (1985, p. 137) observed: "I have used only those characters in which "clear gaps" are found. The overlap in range for at least one (and preferably both) species must not exceed the mean of these adjacent species for distinct character states to be recognized." Hart's approach raises three related issues. The first is that the *removal* of a species may make what were "clear gaps" less evident (fig. **4D**). The second is that means could have been replaced by modes or some other measurement, and this might change the pattern of

overlap. The third is that as with methods discussed earlier, extensive overlap in a character between two taxa may still remain, yet those taxa may be assigned to different states, clearly not a desirable feature.

Almeida and Bisby (1984) advocated a rather stricter approach to the problem of overlap. Ranges, medians, and first and third quartiles for the continuously quantitative variables are needed. Taxa are ordered by increasing medians; boundaries between states are placed either where there were clear gaps between ranges or, at worst, where there are gaps between quartile bars. Even in this worst case, they felt that the assignment of only a few individuals to states would be ambiguous; the assignment of states to species would not be ambiguous. As they emphasized (loc. cit., p. 407), data were being considered in the context of the variation shown by individual taxa, not from some generalized statistical properties of the ensemble of taxa.

There have been several attempts to subdivide variation that lacks absolute gaps by using a variety of statistical manipulations. These have been extensively discussed in recent literature (Archie 1985; Chappill 1989; Pimentel and Riggins 1987; Gowan 1990 presents a careful application) and I do not intend to treat the different methods that have been proposed in any detail. Mickevich and Johnson (1976) developed a technique called gap coding (simple gap coding: see Archie 1985, also references therein). Taxa were ordered by the means of a particular variable; states were recognized when adjacent means differed more than pooled within-group standard deviation (s_p), which Archie multiplied by a constant (c). The choice of gap size, hence the number of states and even whether there were any states, depended on the magnitude of this arbitrary constant.

Simon (1983) proposed the technique of homogeneous subset coding. Taxa were analyzed, one character at a time, using an a posteriori multiple comparisons test; sample sizes had to be large enough to calculate within-group variances. Homogeneous subsets formed the basis for delimiting character states.

Thorpe (1984) developed a method of "divergence coding." Here states were determined by the number of significant differences between taxa in a general comparison. The number of states assigned to each taxon depended on the number of other taxa with significantly different means; this first number was thus affected by the addition of taxa with means identical to those of taxa already in the study.

Both these methods were vulnerable to the addition of taxa with intermediate values, and this was a reason why Archie (1985) proposed recognizing states using generalized gap coding. The first step consists of calculating $s_p{}^c$ again, and ordering taxa by ascending means. Then the first discriminant subset of taxa is produced; this includes those taxa the character means of which are included within $s_p{}^c$ of the mean of the first taxon. The same $s_p{}^c$ was added to the mean of the next taxon; if all taxa with means within that figure were included in the first subset, the second taxon was placed in that subset; if not, it formed a new subset. Character states are coded from subset membership (Archie 1985; Goldman 1988). Because the subsets are delimited with regard to statistical properties of the whole group of taxa, taxa placed in different subsets may be closer than those placed in the same subset, and, as Chappill (1989) showed, increasing the value of c did not have easily predictable results, the number of subsets sometimes increasing.

Chappill (1989 and references) used a form of segment coding in which the number of states is proportional to the variability of the character; the segments (states) being $s_p{}^c$ long. It reflects relative difference between taxa better than the other methods, but, as with many methods that depend on statistical properties of the group of taxa as a whole, it may not reflect details of the pattern of variation within individual taxa or between similar (as judged by means) taxa particularly effectively.

Authors using these methods commonly weight ("scale") characters inversely to the number of states they contain (but see the Discussion for the dubious rationale behind this). There is a feeling that neither too few nor too many character states should be recognized. The former situation would occur if no character states were recognized; the latter, if every taxon were placed in a different state (e.g., Archie 1985; Goldman 1988), with the cladogram suggested by that character alone being more or less highly pectinate if the states are scored as being ordered, as is generally the custom.

Discussion

It is common to emphasize that cladistic analyses are more explicit compared to their phe-

netic and evolutionary forebears. Clearly, however, the delimitation of character states is still for the most part either not explicit, or, if explicit, apparently arbitrary. The preceeding sections demonstrate both the extent and the seriousness of the problem caused by the use of more or less continuously varying quantitative characters in botanical phylogenetic analyses. Such characters are common in morphological data sets, and characters such as genome "types" may also be of a similar nature (Kellogg 1989).

Of course, it is possible that only part of the variation being analyzed is represented by the terms used or the measurements given. Decisions that seem weakly supported when simply reading descriptions may have a much stronger evidential basis (for examples of this, see Ball and Maddison 1987). There is currently no evidence that this phenomenon is widespread, and to the extent that it does occur, characters should be redescribed or remeasured.

Characters with an obvious continuous quantitative basis often show higher homoplasy than others. Levin (1986b) found that there was no significant difference between the consistency indices between characters taken from leaf architecture, epidermis, or leaf anatomy (analysis of variance, $P = >0.05$) in the Euphorbiaceae–Phyllanthoideae. However, 14 of the less quantitative characters he used (this subdivision of characters was carried out without looking at consistency indices; autapomorphies were excluded) showed an average consistency index of 0.34, and 22 more quantitative characters an average consistency index of 0.19. Similar results have been reported by Chappill (1989), Stuessy (1979), and others. This may be a reason for distrusting such quantitative characters, but, because they are relatively common at the generic level and below, it is difficult to avoid using them. [Sanderson and Donoghue (1989) attempted to exclude data sets with quantitative characters from their comparative study of homoplasy levels in cladistic analysis, so one feature that might cause a correlation between homoplasy and taxonomic level of a phylogenetic study may have been excluded. However, some of the studies they included, for example that by Campbell (1986), are almost entirely based on meristic and continuous quantitative characters, while those of Anderberg (1986) and Funk (1982) include many pseudoqualitative characters. As it is clear that the conventional distinction between two classes of characters does not hold, we need more information about the data in the component studies before comparisons can yield precise generalizations.]

Although several authors have tried to exclude quantitative characters from their studies, or to include them only in resolving relationships that were left unresolved in an initial analysis, these restrictions are clearly insufficient. For although obviously quantitative characters are a minority in most cladistic studies, some are nearly always used, and most that I analyzed suffer from serious problems if it is assumed that character states are separated by discrete gaps. The exclusion of such characters from phylogenetic analyses would most likely reduce their resolution (see below), perhaps also changing some patterns of relationships. This itself is serious enough, but the larger aspect of the problem is in the numerous so-called qualitatively-varying characters. Although analysis of their variation is difficult, many of them may suffer from the same problems of state delimitation as their more obviously quantitative brethren.

A number of points may be made in connection with the recognition of this basic problem.

1. Discreteness of States and Level of the Hierarchy. Problems caused by continuous variation do not necessarily increase at higher hierarchical levels. In the Bonnetiaceae–Clusiaceae there are many characters with discrete states of use in phylogenetic studies, in fact far more than can be used for *Kayea* or *Calophyllum*, the phylogenies of which are still largely unknown. Characters in the Bonnetiaceae–Clusiaceae such as the position of initiation of phellogen in the stem, although potentially continuous, show no genuine intermediates in the hundreds of species examined. Even so, the simple continuity discussed here remains a problem, as with the character states used to describe the shape of mitochodrial cristae used in a study of eukaryote relationships (Lipscomb 1989). Continuous variation may indeed be a major problem at lower hierarchical levels (Chappill 1989), perhaps connected with the integration of the characters into development and/or with their function or adaptive significance for the plant (see also Stuessy 1990, table 24.3).

2. Discreteness of States and Size of Study Group. Increasing the size of the study group may affect, in ways that are quite unexpected, whether or not characters show continuous

variation. Attempts to resolve the phylogenetic relationships of too many hierarchical levels simultaneously can affect the pattern of variation of characters and hence the delimitation of their states (Stevens 1987). Evolution proceeds differently in different lineages, and discrete patterns of variation of a character in one lineage may be blurred by variation in that same character in another lineage. Van Welzen (1990) subdivided *Guioa* (Sapindaceae) into subgroups so the analysis of one group would not be affected by the homoplasies in another; more particularly, such subdivision may be necessary to partition variation so that character states can be delimited.

3. Relationship Between the Delimitation of States and Phylogenetic Hypotheses. As we have seen, in many cases different varieties of one species are assigned the same state, despite the variation actually described. It seems to me that these are not simply "mistakes," rather, they suggest that the early steps of phylogenetic analysis are rather different from what is usually supposed. The conventional model, i.e., "first select a monophyletic group, then record variation, then circumscribe the states and decide on their polarity, then analyze the data and provide a hypothesis of the phylogeny of the group" is an oversimplification. Although such a simply linear model is unlikely to be followed in practice, and indeed should not (e.g., Hull 1967; Neff 1986), the problems with delimiting character states when variation is continuous suggests an extreme deviation: even at early stages in an analysis states are delimited so as to circumscribe groups of taxa that are believed to be related.

Even when authors mention the difficulty of using quantitative variation in phylogenetic studies, the variation of those characters used in many cases is a continuum, or there may be alternative ways of subdividing it; reasons for delimiting states are rarely provided. Yet the absence of ideas of relationship, there are no obvious reasons for dividing continua in one place rather than another. Such ideas may spring from the patterns of relationship suggested by one or two characters that the author consciously or unconsciously considers to be of probable phylogenetic importance. I was certainly doing this when I thought that embryo size in the Clusiaceae could be divided at the 4 mm mark; i.e., I was treating as deviant all taxa of *Clusia* with embryos longer than this and all taxa of *Garcinia* with embryos shorter than this. I had no reason for doing so other than my belief that the genera were not closely related (they are often placed in different tribes). Likewise, infraspecific taxa of one species are presumably so frequently misscored because of a belief that they are closely related; there will be a reluctance to assign them to different states.

The result of such a procedure is not necessarily an incorrect phylogeny; it is, however, difficult to work out just what the reasons are for delimiting the boundaries of the states. The division of a continuum into states congruent with a phylogeny suggested by other characters should occur only *after* the production of an initial phylogeny. Failure to discriminate between states that generate groupings and those that are circumscribed only with reference to such groupings greatly confuses the evidential support for phylogenies (but see Maddison et al. 1984). It might be argued that in fact states are never recognized before *some* ideas of relationships have developed in the mind of the investigator, but the pattern of treatment of continuous variation described here suggests far more extensive interaction. Clearly, it is difficult to defend the coding of varieties (for example) to agree with their presumed relationships, i.e., so that all varieties of one species have the same state.

4. Quantitative Characters, Resolution of Trees, and Parsimony. Archie (1985), Chappill (1989), and Thiele and Ladiges (1988) found that the stricter the criteria for the recognition of gaps, the fewer the characters that could be used, and the poorer the resolution of the cladogram obtained. Archie (1985) also noted that relatively few equally short trees tended to be formed using character states produced by techniques such as generalized gap coding. It is indeed possible to produce a more highly resolved phylogeny by using quantitative characters, but what significance is to be attached to this phylogeny? Was it worth the effort? What price increased resolution?

But another problem develops. The fractional weighting of quantitative characters that have large numbers of states produces states with fractional values, or the variation is described using many characters of unitary range. The "most parsimonious" tree produced by analyzing such data may be only very slightly shorter than the next—either a fraction of a step shorter, or a full step longer but in the context of a

tree with a considerable overall length (Chappill 1989 noted this possibility, but did not comment on it). Although it is difficult to justify preferring a tree that is not the shortest available, such justifications can be made, especially if a tree is only slightly longer. This, however, questions how ideas of parsimony are to be applied. If *the* most parsimonious tree is not accepted, criteria that allow one to consider either individually or as contributing to a consensus solution, trees that are within one step (or more) of the most parsimonious tree (see also Bremer 1988) will have to be developed.

Chappill (1989, p. 231) after comparing a number of the more statistical methods, concluded on a profoundly ambivalent note:

> "The philosophical objections to, and practical coding problems for, the use of continuous characters in phylogenetic analysis lead to the conclusion that, wherever possible, they should be avoided since they may introduce an unacceptable level of distortion into analyses in relation to the amount of increased resolution they provide. All available methods of coding quantitative characters for phylogenetic analysis result in some distortion of relationships between taxa. It would be desirable to be able to judge the point at which the noise this creates in the analysis begins to override the useful information added."

5. The Nature of Use in Phylogenetic Analyses. The assumption underlying some of the more statistical approaches mentioned above is that all, or most, different measurements represent information of phylogenetic interest, and that change of a character over time is represented by the total of a number of small changes (cf. Sneath and Sokal 1973; see above). Whether or not the states are discrete at the phenomenological level, there is an assumption that they represent underlying change, perhaps even a discontinuity. This is not incompatible with what we know about evolution (e.g., Edwards et al. 1987). Proponents of techniques for producing character states from continuous quantitative variation frequently discuss the possible loss of information if the characters are not used, or not divided into enough states (Archie 1985; Chappill 1989; Goldman 1988; Thiele and Ladiges 1987). However, if the measurements that have been made are not used in a particular phylogenetic study, this does not necessarily mean that "information" is being lost. Measurements only become information when they are appropriately evaluated. Taxonomic pattern in general, and in particular patterns of potential phylogenetic interest, depend on the hierarchical context in which they are evaluated (e.g., Farris 1969; Felsenstein 1985).

The requirement for sharp gaps between character states has been treated as a methodological requirement of cladistic analysis. It, too, is not incompatible with the results of evolutionary change; change in several genes with small effects will result in discrete gaps, just as will change in few genes with much more pronounced effects (for reviews of the importance of the latter, see Hilu 1983; especially Gottlieb 1984, 1985). Felsenstein (1988a) suggests that there is an assumption implicit in the discrete coding (he includes statistical methods in his discussion) of quantitative variables (characters): that gaps are points or zones of the quantitative scale that natural selection finds it "difficult" to pull the population (sic) across. (There is rarely evidence on whether taxonomic species in plants are single populations, and this is indeed unlikely in many cases.) If character states derived from continuously-varying characters are not given the same weight as those in which the variation is not continuous, this adds another level to this assumption. States of the first kind of character still in principle represent underlying discrete variation, so if they are fractionally weighted, this is tantamount to an assertion that they are not as "important" as states separated by discrete gaps (see also Mickevich and Farris 1981 for discussion bearing on this point). Although a possible weighting criterion is the degree of discreteness of character states, rather than their number, given the nature of taxonomic data, it is hard to imagine how to justify this unambiguously. Indeed, Felsenstein (1988a) observes that gaps in quantitative variables may result from random factors (see also Bookstein 1988). He thus raises the issue of whether all gaps are equivalent, which leads to the problem of weighting again (Felsenstein and Sober 1986). But if a species is a multipopulational unit, then gaps in variation between such species are less likely to be the proximal result of such random factors.

Felsenstein (1988a) also notes that none of the authors dealing with coding methods has suggested tests for the presence of underlying discrete states, although genetic studies and common garden experiments to control for phenotypic plasticity can be carried out, as Campbell (pers. comm.) notes. This emphasizes sev-

eral issues: 1) If there are such states underlying each "different" taxon measurement, all gap coding methods discussed recognize only some of the states. 2) There is no reason to suppose that all measurement differences convert to underlying evolutionary steps. 3) Whatever coding method adopted, the basic assumption is usually that different states represent qualitative differences, at some level, at least. 4) Discrete changes at the molecular level may not be evident as such at the particular observational level adopted. 5) Whether or not underlying states are represented phenotypically by absolute gaps, overall congruence of data is one way we can "test" for their existence. We need to compare analyses based on carefully evaluated gap coding with those based on exhaustive manipulation of continuous quantitative characters, and those based on molecular data. Such comparisons have not yet been carried out (attempts along these lines need re-evaluating in the light of the problems outlined here, cf. Richardson 1983 and Whalen 1978). Indeed, the comparison of data sets of different sizes and types is not a simple matter of comparison of homoplasy level.

In any event, clear justification of the circumscription of the character states that we use in our attempts to produce a phylogeny (and in phenetic studies; this problem is not restricted to one systematic philosophy) is essential. Phylogenies without this basic justification are intrinsically of much less biological interest than they might otherwise be (see also Mitter, in Coddington 1987); sophisticated data manipulation avails for little if the data manipulated are suspect.

What guidelines can be offered to deal with this series of problems?

1. *As a general rule, character states used in phylogenetic analysis should be discrete and without overlap.* Adherence to this rule should not be mindless; absolute gaps should not automatically be taken as evidence for the existence of states. Statistical tools such as standard deviations, means, and modes may provide a feel for the structure of infrataxon variation. The production of character states from continuous variation seems of dubious utility if it is based on statistical properties of the ensemble of the taxa under study. If such characters are used, it is difficult to justify scaling them inversely to the number of states that they contain. Procedures such as reducing variation to means alone before deciding on the limits of states have little to recommend them. If taxa placed in different states are more similar (in that character) than they are to the most similar taxa placed in the same state, then the criteria for delimiting states may be suspect.

Discrete states may be produced in a variety of ways.

A. Variation can be analyzed in the context of phylogenies of the terminal taxa *before* decisions are made as to the existence and circumscription of character states; it must then be possible to hypothesize that these terminal taxa are monophyletic. A rare variant may be ignored if it is a reasonable assumption that the taxon in which it occurs is not basal and paraphyletic within the terminal taxon.

B. One (or a few) taxa that blur the boundaries between what are otherwise clearly discrete states should be scored with care. It is unwise to score such taxa as having only one of those states, or to add a separate state that includes only intermediates. Scoring such taxa as having missing data, or as having both states, may affect the consistency index of cladograms.

C. Variable characters may be excluded from the initial phylogenetic analysis, their division into states being considered in the context of lower level analyses.

D. Variation in the outgroups must be taken into account in the delimitation of states; variation in outgroups may throw doubt on the significance of discrete states in an ingroup.

E. Somewhat more generally, all variation needs careful evaluation. In certain circumstances, outlying variation can be ignored (a particularly large measurement is taken from a sterile specimen—did that specimen come from a sapling?). Taxa with larger measurements for a particular character tend to be absolutely more variable than taxa with smaller measurements.

2. *The justification of character states should be far more extensively documented than at present.* This recommendation entails a change in both reviewing and editorial practice. Because the basic data of phylogenetic analyses are character states, more space should be devoted to the justification of the delimitation of these states. The reader is all too often simply presented with lists of character states, or there may be brief mention of the extent of the variation of a particular character. As we have seen, even

when claims are made that character states are delimited by the point of inflection of a curve of the variation, this may not be evident on inspection of the data. It seems wiser to assume that morphological variation is potentially continuous than the reverse. In some cases the requisite documentation of the existence (or otherwise) of character states is quite simple (e.g., Almeida and Bisby 1984). In less obviously quantitative characters, attention should first be paid to analyzing the basic variation, only later seeing how that variation pattern can be expressed using conventional descriptive terms. We should not assume that these terms represent discrete variation in the real world.

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APPENDIX. Quantitative characters and ingroup variation.

Included here are further examples showing how character states in quantitatively varying characters are delimited, as well as further details of some of the examples already mentioned. Although no new points are raised here, the examples confirm the pervasiveness of the problems under discussion.

Of the three continuous quantitative characters Todzia (1988) used in her study of *Hedyosmum* (Chloranthaceae), one, the length of the tips of the floral bracts [tips 1–2 mm (0), 2–6 mm (1), 16–28 mm (2)] showed continuous variation. Another, fusion of perianth lobes [free to the base or partially united (0), completely united (1)], apparently showed substantial variation. The perianth was described as being at least ¼ fused in the species belonging to the *macrocarpa* group, for which the state of fused perianth was an apomorphy. It was also described as being at least half fused for six of the 20 species of the *microcarpa* group, and as "basally united" in another seven species; the *microcarpa* group was considered to be plesiomorphic for this character. However, the overlap here may be due more to the way the character was described than to the character states (Todzia, pers. comm.). A third character, the length of the petiolar sheath, presented an even more complex situation. The three states recognized were <0.3 cm [0, known only in the outgroup, *Ascarina* (Chloranthaceae)], 0.3–1 cm (1), and usually >1 cm (2; fig. 4A). Todzia (1988,

p. 37) noted that *H. correanum*, *H. burgerianum* (both in the *microcarpa* group), and *H. cumbalense* (of the *macrocarpa* group) "occasionally have individuals with some leaf sheaths less than 1 cm long, but the majority of individuals have leaf sheaths longer than 1 cm." However, the midpoints for this character in all three species are below 1 cm, and the entire range of variation of the first-named species is below this figure. Other species in the *microcarpa*, *grisebachii*, and *pseudandromeda* groups show similar variation.

A phylogenetic study of the relationships between species of *Crusea* (Rubiaceae) used a data set of some 58 characters (see Estabrook and Anderson 1978; data from Anderson 1972). Estabrook and Anderson (1978, p. 180) described as ". . . 58 qualitative characters, . . . each serving to divide the 17 EU's [evolutionary units] into one to many non-overlapping classes called character states." There are 27 continuous quantitative characters, at least eight more of which are generally ratios or proportions in which the states are described in words rather than numbers (e.g., relative width of cotyledons was divided into four states: very narrow, narrow, wide, and very wide), and a further four discrete quantitative characters. Anderson (1972) provided averages for the 10–30 measurements of each character, and Estabrook and Anderson (1978) later used these averages to delimit character states. Variation in eight continuous quantitative characters is shown here (figs. **1M**, **3G**, **H**, **5A-E**); there are few obvious breaks in the variation.

Simpson (1989; fig. **5F-H**) monographed *Krameria*, of the Krameriaceae. She used three continuous quantitative characters. In the character of amount of petal fusion (fig. **5F**), *K. tomentosa*, with less than 5% fusion, is separated from *K. bahiana*, which has "essentially free" petals. The major gap in the variation would seem to unite these two species in the same state. Similar demarcation problems occur in the character of leaf length in particular (fig. **5G**).

Judd (1984), in his study of the American species of *Agarista* (Ericaceae), divided states to minimize the number of taxa with two states, although he did not score taxa that straddled states as being intermediate. Variation in calyx lobe length (fig. **5I**) showed a sharp inflection. Three other characters are more problematical. Seed length [usually 2 mm or more (0), usually 1.5 mm or less (1); fig. **5J**]; inflorescence length, petiole length, and leaf length [usually >3 cm long (0), usually <2.5 cm long (1); fig. **5K**] all show largely continuous variation. The latter character in particular has alternative break points in the variation, the adoption of which depends on variation in the outgroup and details of the variation pattern of individual species. [Leaf size may provide information of potential phylogenetic interest; the very small leaves of *Pieris nana* (Ericaceae), less than 1.5 cm long, is a state distinct from the much larger leaves of the other species in that genus (Judd 1982), at least looking at variation in the ingroup alone.] A final quantitative character used in the study of *Agarista*, corolla size, was divided into two states: less than 13 mm long (0) vs. often more than 13 mm long; it, too, shows some overlap, even though it is a simple autapomorphy for *A. oleifolia*. In *Craibiodendron* (Ericaceae), Judd (1986) recognized two states in the meristic quantitative character: the number of flowers on the secondary axes of the inflorescence, 7–30 flowers (0) vs. 1–6 flowers (1). The variation can be divided into two states.

The single continuous quantitative character used by Akinama (1988) in his study of *Lespedeza* (Fabaceae), whether the wings were longer than the keel, showed a sharp break point.

In the study of the phylogeny of *Agastache* (Lamiaceae; Sanders 1981; data in Sanders 1987) two suites of characters were used: one for the initial general analysis, and the other to subdivide groups that remained unresolved in this general analysis. Characters used in the general analysis include inflorescence internode length [equal or longer than the calyx (0), much shorter than the calyx (1)]; degree of connation of the upper calyx teeth (fig. **5L**); and ratio of bracteole length to cyme internode length [1.5 or greater (0), 1.0 or less (1); fig. **7C**]. There is a breakpoint in the variation in the last character, less in the others.

LaDuke (1982) also expressed reservations about the use of quantitative characters in *Tithonia* (Asteraceae). The variation in one such character that he did use, that of pale length [with states "short" (0) and "long" (1); fig. **6F**] confirms his reservations: no clear break in the variation is evident. The state "long pales" was the only synapomorphy for one of the basal lineages in the genus. Another quantitative character, ligule length [also with states "short" (0) and "long" (1); fig. **6G**], is divided at a break point in the variation, but is perhaps also divisible elsewhere.

Jansen (1985) found variation within a few taxa of *Acmella* (Asteraceae) was so extreme that possible states of characters such as the shape of the phyllary apex were blurred; these characters could not be used in the cladistic analysis. One continuous quantitative character that was not an autapomorphy was peduncle length (fig. **6A**). Even here, infrataxon variation was considerable, and problems caused by overlapping variation and irregular scoring are evident. The derived state was a synapomorphy for a major clade and lacked homoplasy; however, this clade was also supported by the synapomorphy, fascicled roots, which showed only a single reversal.

Stuessy (1979; data from Stuessy 1972) tried to avoid the use of quantitative characters in his study of *Melampodium* (Asteraceae), adding them only to resolve portions of the tree. However, the states of these characters were evaluated with respect to the variation in the whole genus. The problems Stuessy faced are evident in the descriptions of the states, features such

as ray floret number being subdivided [ray floret number <5.5 (1), 5.5–10.1 (0), >10.1 (2); see fig. **6C**]. The variation of this and other characters, leaf length (fig. **6B**), fruit length, plant height, and head diameter (fig. **6D**), all show variation that is continuous, or nearly so.

Characters of *Lipochaeta* (Asteraceae; Gardner and LaDuke 1978; data in Gardner 1979) were divided into discrete states, and the relationships of the diploid and polyploid species of the genus were analyzed separately. Twenty of the 32 characters used were continuous quantitative characters, the states in the diploids and tetraploids being different; for the apparently qualitative characters the states in the two groups were the same. Analysis of five quantitative characters from different parts of the plant (figs. **3J-L**, **4B**, **C**) suggests that discrete states are hard to come by in both diploids and tetraploids. A similar pattern of variation occurred in the meristic quantitative character, number of pappus bristles in *Pegolettia* (Asteraceae; Anderberg 1986).

In *Drimia* (Hyacinthaceae; Stidje 1987; fig. **6E**) three states of the character of corolla lobe fusion were recognized: none (0), slight (1), and strong (2). In some individuals of all species scored as having slight fusion there was in fact no fusion, so the existence of discrete states is compromised. Two discrete states based on corolla length (<4.5 mm vs. >4.5 mm) can be recognized, as well as two states of a character based on corolla lobe fusion (none + slight vs. strong).

Kress (1984) included several quantitative characters in his study of Central American species of *Heliconia* (Musaceae). Perhaps rather surprisingly, variation in stem height allowed the recognition of two states, >4 m tall (0) and <4 m tall (1), although measurements were recorded only to the nearest 0.5 of a meter. Only one species, *H. xanthovillosa*, with stems 3.5–4.5(7) m tall, showed overlap; it was scored as having the plesiomorphic condition. Two other quantitative characters, inflorescence size (as measured by the number of bracts; fig. **6H**), and the index of pollen polarity also showed more or less clearcut break points.

Other quantitative characters used by Kress present problems. The character of length : width quotient of cincinnal bracts might be divisible in an additional place (fig. **6I**), but it is difficult to decide on what is a significant gap when the data are points rather than ranges; nearly all points are separated by gaps of one size or another. Three other characters show largely continuous variation. These are pollen equatorial diameter (fig. **7F**), pollen polar diameter (fig. **7K**), and overall pollen shape. Confusion the issue here is the fact that some taxa show extreme variation and others none at all; sample size for these characters was small.

A few continuous quantitative characters were used in a study of *Hexaglottis* (Iridaceae; Goldblatt 1987). The characters are the length of the hypanthium tube, divided into two states, the latter in turn subdivided: hypanthium absent (0), >1 mm long (1); hypanthium 1–2 mm long (0), >3 mm long (1). The circumscription of these states presents no problems. Similarly, the character of degree of connation of the filaments [connate at most only in their lower half (0), entirely united or free only at the apex (1)] shows a sharp break when the six species of *Hexaglottis* and the 31 species of *Homeria* are considered. The filaments of none of the former genus are more than 50% connate, while those of only one species of the latter are as little as 70% connate, most being entirely connate (Goldblatt 1981, 1987).

Campbell (1986; data in Campbell 1983) gave a detailed analysis of variation in *Andropogon* (Poaceae). He expressed doubts about the usefulness of converting continuous into discrete variation for phylogenetic analysis, but divided continuous quantitative characters into states where there were gaps in the variation (Campbell 1986). Variation in four characters is illustrated (fig. **7A**, **B**, **D**, **E**); again, gaps seem hard to come by, and scoring of variation in infraspecific taxa also presents problems (fig. **7A**, **E**). Other characters are not graphed here—anther length, raceme length, raceme sheath length, peduncle length, ligule length, length of ligule ciliation, and plant height—show similar patterns of variation.

Five quantitative characters were used by Meerow (1987) in his study of *Eucrosia* (Amaryllidaceae). There is a sharp discontinuity in petiole length [short (0), long (1); fig. **7G**] and a somewhat less clear discontinuity in the number of flowers per inflorescence (fig. **7H**). States in other characters, including the length of the tepalline tube relative to the free tepals [tube longer than (0), nearly equalling (1), or shorter than (2) the free tepals; fig. **7I**], the development of the staminal cup [conspicuous or rarely reduced (0), reduced (1), absent (2)], and the longest equatorial diameter of the pollen (fig. **7J**), are more problematic. In the first character in particular there is little intrataxon variation, and so deciding on the boundaries of the states is difficult.

Hennipman and Roos (1982) provided extensive documentation for characters they examined in their study of *Platycerium* (Polypodiaceae). The states of quantitative characters such as the length of the rays of the stellate hairs, the mean width of the rays of the paraphyses, and the mean length of these rays, seem substantially different, but because only means, not ranges, were given, evaluation of the nature of the gaps is difficult (ibid.; figs. 7, 8). Ranges were given for characters such as the number of rays of stellate hairs and the number of epistomium cells in the sporangia (ibid.; figs. 5, 9); these were excluded from the final analysis because of extensive overlap. One character for which ranges were given, the number of indurated cells in the annulus, showed a distinct breakpoint in the variation (ibid.; fig. 9), and was used in the final study.

Note added in proof: J. S. Farris in a recent paper ("Phenetics in camouflage," Cladistics 6:91–100. 1990.) suggested that attempts to scale characters with many states, i.e., to consider all multistate characters as having unitary ranges, had little merit. He also clarified problems entailed by the use of Archie's generalised gap coding method. He showed that two taxa might differ in the states to which they were assigned despite there being no statistically significant difference in the measurements of those taxa for that character; this was also true, although to a lesser extent, with generalised subset coding. The use of procedures in which differences attributable to sampling error could produce "evidence" of monophyly did not seem justifiable. G. C. D. Griffiths ("On the foundations of biological systematics,"Acta Biotheor. 23:85–131. 1974, see pp. 108–113) recommended replacing descriptions of sense qualities with descriptions of real attributes, and as far as possible expressing the latter in terms of measurements.