A Critique of "Bromeliales, Related Monocots, and Resolution of Relationships among Bromeliaceae Subfamilies"

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A Critique of “Bromeliales, Related Monocots, and Resolution of Relationships among Bromeliaceae Subfamilies.” In a recent article by Gilmartin and Brown (1987), the interrelationships of the three defined subfamilies of the Bromeliaceae were studied using both phenetic and cladistic analyses. It is their cladistic analysis that I wish to address. As noted by the authors, one of the major difficulties with cladistic studies is determination of the evolutionary direction (polarity) of character state transformations. The outgroup method, which is generally accepted as that most valid for determining character polarity, is often problematic in that the closest outgroups of the ingroup are usually not known with any degree of certainty. Gilmartin and Brown do utilize outgroups in their cladistic analysis both for assessing the interrelationships of the subfamilies of the Bromeliaceae and for determining the sister group to that family. However, I do not believe their specific methodology is valid.

Gilmartin and Brown selected ten families of monocotyledons as the possible outgroups. This was wise because the interfamilial relationships in this complex have not been definitively established (e.g., compare the cladograms/phylograms of Dahlgren and Rasmussen 1983, and Dahlgren and Bremer 1985, with that of Walker 1986). The three bromeliad subfamilies were treated as separate O.T.U.'s, and a “hypothetical monocot ancestor” (curiously undefined in their character/taxon matrix) was used to root trees. The authors performed cladistic analyses using PAUP, version 2.4 (Swofford 1983) with assignment of states of all twenty characters as unordered. The major methodological error of this study is that each of the ten hypothetical outgroup families was treated individually with the three bromeliad subfamilies in separate parsimony analyses. The premise of the authors was that the most likely resolution of the ingroup and of the sister group to the ingroup is that indicated by the most parsimonious tree which is both shortest in number of state changes and has a high (but not necessarily highest) consistency index. The flaw of this premise is demonstrated in the following example.

Consider the data matrix of figure 1a, which lists three outgroups (X–Z), the ingroup (comprised of the sub-taxon D–F), and a hypothetical ancestor (ANC). If a cladistic analysis is conducted in which all three putative outgroups are included, then the most parsimonious cladogram for all taxa is that of figure 1e. This cladogram indicates that outgroup Z is the sister group to the ingroup and that the most parsimonious topology for the ingroup is (D(E,F)). If, however, each of the outgroups is individually analyzed with the ingroup and ancestor (as done by Gilmartin and Brown), the resultant most parsimonious cladograms are illustrated in figures 1b–d. The tree that is both shortest (length = 23) and has the highest consistency index (C.I. = 0.957) is that seen in figure 1b, in which outgroup X is analyzed alone with the ingroup. In contrast, the trees of figure 1c and 1d are both longer and have lower consistency indices. Thus, according to the reasoning of Gilmartin and Brown, because the cladogram of figure 1b is shortest and has the highest C.I., then the most likely sister group to the ingroup is taxon X and the best supported ingroup resolution is (F(D,E)). However, the global analysis, including all outgroups, indicated both a different ingroup topology and a different sister group (closest outgroup) to the ingroup. From an inspection of the cladogram at figure 1e, the cause of this apparent inconsistency can be seen. First, an erroneous designation of the sister group can occur if the “true” sister group (from the global analysis) shows a certain degree of convergence with a member of the ingroup. Because of these convergent state changes (characters 14–18 in fig. 1), a cladistic analysis treating only that sister group with the ingroup may show a greater length and lower consistency index (cf. fig. 1d) than one treating only an earlier diverging outgroup (showing less convergence) with the ingroup (cf. fig. 1b). Thus, the occurrence of a short length and high consistency index indicates only that the outgroup under consideration shows little or no character convergence with the ingroup; this outgroup may or may not be closely related to the ingroup. Second, even when the ingroup is clearly monophyletic, differing ingroup topologies can occur between a global analysis versus one treating a single outgroup if one or more derived states are shared between the true sister group and some (but not all) members of the ingroup. For example, in figure 1 the ingroup topology from the global analysis (fig. 1e) differs from that of figure 1b, which has the shortest length and highest C.I., because characters 19–20 are synapomorphic for taxa Z and D–F in figure 1e (with a reversal in the clad to taxon F) but, with the elimination of outgroup Z, they are synapomorphic for only D and E in figure 1b. Because the possibilities both of convergence between the sister group and an ingroup member and of reversal within an ingroup clade are very possible (and likely to be encountered) in cladistic analyses, the reasoning of Gilmartin and Brown appears faulty.

The hypothetical example of figure 1 was constructed to “force” the monophyly of the ingroup (D–F) in all most parsimonious trees. Figure 2 shows an example in which the monophyly of the ingroup is in doubt. From the data matrix of figure 2a, the most parsimonious cladogram in a global analysis, including all outgroups (X–Z), is that of figure 2e. This tree splits the pre-designated ingroup such that taxon E is most closely related to outgroup Z and taxon D is most closely related to outgroup Y. If each of the
outgroups is treated individually with the ingroup, however, the resultant most parsimonious cladograms are those of figure 2b–d. The cladogram of figure 2b is shortest and has the highest consistency index and would, by the logic of Gilmartin and Brown, be accepted over the others as showing the most likely interrelationships of the ingroup. Thus, in this example, they would argue both that the ingroup is monophyletic and that taxon X is the sister group to the ingroup; however, the most parsimonious global
Fig. 2. a. Hypothetical data set for outgroups X–Z, ingroup taxa D–F, and ancestor ANC. b–d. Most parsimonious cladograms including ingroup, ancestor, and only outgroup X, Y, or Z. Figure 1b has the highest consistency index (C.I.) and the smallest length and indicates the ingroup to be monophyletic. e. Most parsimonious cladograms including ingroup, ancestor, and all outgroups. Note that the monophyly of the ingroup is not supported. C = convergence; R = reversal.

analysis of figure 2e supports something quite different.

These examples are parallel to, and would appear to invalidate, Gilmartin and Brown's (1987) conclusions that: 1) the Bromeliaceae is monophyletic, 2) the Velloziaceae is the most likely sister group to the Bromeliaceae, and 3) the subfamilies Bromelioideae and Tillandsioideae are sister taxa. They might have chosen to present a global parsimony analysis (Maddison et al. 1984) using all ten outgroups, with or without the hypothetical monocot ancestor. However, my own global analysis using their data set resulted in a significant splitting of the ingroup, although I could not be certain of the coding of the
hypothetical monocot ancestor. This is despite the contention by the authors that the monophyly of the Bromeliaceae is well supported from their own studies and those of others. Gilmartin and Brown’s methodology shows some resemblance to the outgroup substitution method of Donoghue and Cantino (1984). Outgroup substitution, however, involves the use of different combinations of outgroups (not just one outgroup) to assess polarity of characters. Cladistic analyses are run using various character polarity sets to assess congruence among the cladograms. Donoghue and Cantino emphasized, however, that the attainment of a certain topology of the ingroup most of the time (similar, e.g., to the majority occurrence of a Bromelioidae–Tillandsioideae topology in Gilmartin and Brown’s study) does not in itself argue that it is valid, as distantly related outgroups may have been used most of the time.

Another problem with the analysis of Gilmartin and Brown is their use of the “hypothetical monocot ancestor” to root trees. This hypothetical ancestor was, unfortunately, unmentioned and undefined in the character/taxon matrix. Because the polarization of character states was crucial to a resolution of the phylogeny of bromeliad subfamilies (and a major objective of the paper in itself), the rationale for defining this ancestor should have been a focus of the paper. More importantly, it should be realized that outgroup analysis itself is performed to determine whether character states of the ingroup taxa are ancestral or derived (with reference to the outgroup node; see Maddison et al. 1984). Gilmartin and Brown’s use of single outgroups along with the “hypothetical monocot ancestor” is, in fact, equivalent to using two outgroups, as the ancestor functions as a second outgroup in determining character polarity. However, this “hypothetical monocot ancestor” is presumably a collection of ancestral states for the monocotyledons as a whole and would represent an outgroup extremely far removed from the Bromeliaceae. While its use might be valuable in a cladistic analysis of major clades of monocots, it would probably yield faulty information regarding character state polarity among the families of the bromeliad complex.

In addition to the above, there are the following problems with the original data matrix of Gilmartin and Brown. 1) It is unclear why the Strelitziaceae was used as an exemplar for the entire Zingiberales (=Zingiberiflorae, Zingiberidae); it would seem preferable to utilize the ancestral states for the entire order, if possible. 2) Character #4, “stomates”; inclusion of this character provided no useful information in resolving relationships and could have been eliminated; although it was treated as a two-state character, only the first state (“paracytic”) and “missing information” are scored in the data matrix. 3) Character #8, “endosperm”; this character is coded as having three states, but only two are listed in the data matrix. This is probably simply an oversight, as the missing state, “B. plasmodial,” corresponds not to endosperm type but to a type of tapetal development. 4) Character #9, “number of nuclei per tapetal cell”; the two states are defined as “A. mostly 1 or 4” and “B. 2.” It is unclear, however, why the occurrence of 4 nuclei per tapetal cell is grouped with that of 1 nucleus per tapetal cell in state “A.” It would seem more logical to, e.g., group the occurrence of 2 or 4 nuclei per tapetal cell together as a single state (as “multinucleate tapetal cells”). 5) Character #11, “chromosome number”; the rationale for dividing this character into the states “A. n = 25,” “B. n = 8–14, 17, 19, 24,” “C. n = 15, 22, 30” is not explained and seems illogical without additional karyological evidence. 6) Characters #14, “cell wall of foliar scale” and #15, “scale development”; these characters provide absolutely no information in determining cladistic relationships because all outgroups (and presumably the hypothetical ancestor as well) were coded as “missing information”; thus, with reference to the three subfamilies of the Bromeliaceae, a synapomorphy (linking two subfamilies) could not be distinguished from an autapomorphy within a single subfamily, except with reference to the most parsimonious topology deduced from other characters. 7) Character #17, “ovary [position]”; this character was coded as “A. always superior,” “B. superior or inferior,” “C. usually inferior”; only the Pitcairnioideae was coded as having a “superior or inferior” ovary position. However, scoring the Pitcairnioideae alone as having the intermediate state of an unordered series seems questionable because its occurrence would effectively function as an autapomorphy for the subfamily, eliminating the possibility of homology between inferior-ovaried members of the Pitcairnioideae and other inferior-ovaried taxa. Although much controversy exists as to the coding of polymorphic characters, it would seem preferable either to a) eliminate the intermediate state “superior or inferior” and code taxa polymorphic for ovary position as having the (presumably) ancestral “superior” condition; or b) subdivide polymorphic taxa (the Pitcairnioideae in this case) into non-variable, monophyletic units. 8) Character #20, “pollen type”; in contrast to the data matrix, grains are not “inaperturate” in any member of the Haemodoraceae and can be monosulcate, 2–3-porate, or oligoforaminate in that family (Erdtman 1966; Simpson 1983); pollen aperture type is not “unknown” in the Velloziaceae and Pontederiaceae, being monosulcate in the Velloziaceae (Erdtman 1966; however, see Ayensu and Skvarla 1974 re. Vellozia) and disulculate in the Pontederiaceae (Erdtman 1966; Rao and Rao 1961; Simpson 1987).

A better approach in future analyses might be the following. First, a careful character analysis is essential and is the foundation for the entire analysis. It is vital to carefully consider and assess the selection,
definition, transformation, and homology of each character and character state. Although Gilmartin and Brown utilized excellent sources (e.g., Dahlgren and Clifford 1982), some of the characters they selected have an extremely limited data base and others were not well researched. Many more characters than those treated by the authors should be examined. In a cladistic analysis, emphasis should be placed on a discussion of the characters that traditionally have been used to characterize the Bromeliaceae and whether the cladistic analysis supports its monophyly. Second, outgroup comparison using a global parsimony approach (Maddison et al. 1984) or, perhaps, outgroup substitution (Donoghue and Cantino 1984) should be attempted. I would eliminate the “hypothetical monocot ancestor” and attempt to ascertain what is ancestral for the Bromeliaceae. Third, in subsequent cladistic analyses, the Bromeliaceae may be “forced” to be monophyletic (if necessary) by weighting those features hypothesized to represent synapomorphies for that family alone. Assuming the Bromeliaceae to be monophyletic, both the interfamilial relationships and the sister group status of the family could be analyzed using the above outgroup methodologies.

Identification of critical character-state changes among the ingroup and outgroups should be a primary objective of such an analysis. Such cladistic analyses can be especially important in assessing where the data is weak and can serve to determine where future research is needed.

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LITERATURE CITED


—MICHAEL G. SIMPSON, Department of Biology, San Diego State University, San Diego, California 92182.

Response to Simpson. Michael Simpson raises some significant methodological questions in his commentary on our paper concerning the pineapple order, Bromeliaceae, and casts doubts on the systematic results. We will try to clarify exactly why we did the analyses in the manner reported in our paper and why our approach is appropriate with our data. While we wish to avoid becoming embroiled in an endless controversy over alternative cladistic methods, the recommendation of Simpson to rely on global analyses, which we did not do, requires response.

As pointed out in our paper, the Bromeliaceae is an isolated group usually placed in its own order. In addition, there is strong evidence that the family is monophyletic, e.g., their unusual, peltate, foliar scales (Tomlinson 1969; Benzing 1980; Varadarajan and Gilmartin 1987); the conduplicate, spiral stigmas (Brown and Gilmartin 1984, and in manuscript); the distinctive flavonoid chemistry; the base chromosome number of x = 25 (Brown and Gilmartin 1986, and in manuscript). Further information supporting monophyly of Bromeliaceae is given in Dahlgren et al. (1985). For example, (page 330): “Description as for the order. The family is to be regarded as a 'climax group.' Within its combination of characters it has reached an extraordinarily rich variation. The specializations in water economy (the sheaths, the xeromorphic leaf features, the water-absorbing peltate hairs, the water storing tissue, etc.) are the features that are the most striking.”

Two questions were addressed in our paper on the monophyletic order Bromeliaceae. The primary question was the sister taxon status among the assumed monophyletic group of three subfamilies of the bro-
meliad family. To help resolve the first question, we wanted to know the most likely sister taxon to the family.

**Global Analysis.** Among the criticisms of our methods, Simpson focuses on our reliance on cladistic analyses that employ, sequentially, each of ten individual putative sister taxa. We will term this sequential analyses. Simpson prefers to use "global analyses," i.e., all of the taxa in a single analysis (see Maddison et al. 1984 on global parsimony). He provides hypothetical examples with artificial datasets analyzed with both global and sequential methods. Simpson discussed character-state changes on these trees and used results of the global analyses to determine "the 'true' sister group." He assumes that if results differ, it is sequential analysis that is in error. We see no rationale for this assumption relative to our study. Global analysis involves simultaneous resolution of ingroup and outgroups, and as Maddison et al. (1984) state, this requires more extensive data sets than typically are available.

For our bromeliad subfamilies, global analysis would mean using all of our ten putative sister taxa in a single cladistic analysis (with our data set of 20 characters), rather than doing ten separate analyses, as we did. Our initial assumption was that the sister taxon to Bromeliaceae is one of the ten selected taxa. We tried to identify the sister taxon to Bromeliaceae from among several different lineages of monocots.

The ten together with the three subfamilies of Bromeliaceae almost assuredly constitute a grade not a clade; i.e., the ten together do not form a monophyletic group of taxa. As has been pointed out frequently, e.g., Sanders (1981), an important assumption that is inherent in hennigian cladistics is that the study group is monophyletic. We had to cope with the "... common problem of uncertain outgroup relationships" (Donoghue and Cantino 1984).

Prior to writing our 1987 paper, we decided that to employ one analysis of a putative grade in order simultaneously to test multiple hypotheses concerning sister taxon status to Bromeliaceae would be a very dubious endeavor. Therefore we placed no stock in global analyses with our particular data set including ten outgroups.

Simpson agrees that cladistic analyses are suitable for addressing the kinds of questions we addressed. However, for these kinds of questions, Simpson recommends global analysis or, short of this, he recommends the outgroup substitution method, i.e., using various combinations of the taxa.

We have now tried several combinations but we doubted from the start the appropriateness of this approach for there is little a priori support for monophyly of most such groups. Furthermore, such analyses constitute a more complex set of hypotheses than the sequential analysis of one putative sister taxon at a time. We feel justified in hypothesizing that each of the taxa could be the sister taxon and with our method we examine each hypothesis separately. Not surprisingly in view of their probable paraphyletic or polyphyletic nature, results with combinations from among the ten taxa are not encouraging. They portray the Bromeliaceae as a grade not a clade. We emphasize that this family appears to be a closely knit group sharing unique traits, synapomorphies, that are unlikely to have resulted from convergences. The results with the complex test (multiple putative sister taxon in one analysis) are contrary to a significant body of data and constitute a posteriori reasons for not including several putative sister taxa in one analysis.

To summarize, results from the kinds of cladistic analyses favored by Simpson indicated that the group of three bromeliad subfamilies, which a considerable body of evidence indicates is a monophyletic group, is not monophyletic. Given our knowledge about Bromeliaceae (and we are not prepared to ignore this knowledge because of a blind reliance on global analyses that are based on one data set), such results cast suspicion on the cladistic analysis. To clarify this matter, two of the trees that we obtained recently with analyses of the type favored by Simpson are shown in figures 1 and 2. Other analyses using this approach produced similar results in that all separated the subfamilies of Bromeliaceae at least to some degree. Most trees showed homoplasies involving the bromeliad subfamilies (in particular characters 5 and 11). These results are not surprising. Much homoplasy is to be expected to occur when a grade rather than a clade is being analyzed. Secondly, the subfamilies of the Bromeliaceae are separated, yet we know that they share uniquely derived traits, as noted earlier, e.g., chromosome base number, unique foliar scales, unique stigma morphology, etc.

Numerous, equally most parsimonious trees were produced, a result that often occurs when homoplasy is high. Figure 1 with eight putative sister taxa and figure 2 with four putative sister taxa are examples. Other subsets of the ten that we ran also showed dispersion of the members of the assumed monophyletic family. If we had selected monocot families at random to make up the group, we probably would
not have observed much more variation nor more dispersion of the Bromeliaceae subfamilies in the resulting trees.

**Lundberg Rooting.** Lundberg rooting avoids artificial homoplasies that may be caused by the outgroup (Swofford 1985). Using a subset of two putative sister taxa, Strelitziaceae and Velloziaceae, and Lundberg rooting, one parsimonious tree was found (length 21, CI = 0.91). The topology is: Anc{S(P(V(B,T)))}. The same two bromeliad subfamilies, Bromelioidae and Tillandsioideae are sister taxa, supported by exactly the same synapomorphies (10A, 12B, 19B) as when only Velloziaceae was used with the monocot, hypothetical ancestor (see table 3 in our paper). Two of these synapomorphies, 10A and 12B, are the same as with sequential analysis of Xyridaceae and Strelitziaceae described in our 1987 paper (see table 1 and 2).

However, the branch with Velloziaceae and two of the subfamilies of the bromeliad family is only weakly supported by character 16. The characters were unordered and the tree imposes a highly unlikely transformation series for character 16, seed appendage: 16 B—16 A—16 C. The change from conspicuous appendage being entire, 16 B, to absent, 16 A, and thence to divided, 16 C, seems unlikely, i.e., changes from the presence of a conspicuous seed appendage, to lack of the conspicuous appendage, to presence of a divided appendage. (Nor would the reverse direction of this transformation series seem likely.) Thus, there is no strong support on this particular tree for a monophyletic lineage consisting of Velloziaceae as part of the bromeliad subfamily.

While Velloziaceae may be extremely close to the bromeliads, we feel that an analysis with both Velloziaceae and Strelitziaceae regardless of whether or not Lundberg rooting is used, is weaker than an analysis with a single putative sister taxon. The presence of the two putative sister taxa (if these two lineages are not closely related, and everything we know suggest that they are distinct lineages) provides opportunity for the algorithm to create false synapomorphies.

There can be little justification for employing global analyses with our data. For example, as stated in our paper, the Pandanaceae are thought by most phylogenists to represent a very separate, monophyletic lineage. This may or may not be related to elements in Dahlgren's Bromelioliraeae. We included this family in the sequential analyses as one of ten hypothetical sister taxa, but there is no justification, either *a priori* or *a posteriori* for analyzing Pandanaceae together with all (or any) of the nine other families being used in the sequential analyses. Analyzing each taxon, one at a time, examines one at a time each of a series of reasonable hypotheses. To throw these particular taxa together in one analysis is not supportable.

It appears obvious to us that one is not justified in concluding from the results of analyses of the sort favored by Simpson that the Bromeliaceae is not monophyletic. In fact, monophylesis of Bromeliaceae is a prior assumption, based on other data. It is unnecessary to go against a considerable body of evidence that supports monophylesis of Bromeliaceae.

Neither the full set of ten or subsets of these necessarily comprise monophyletic groups and we should not expect correct resolution of relationships among these lineages. Relationships imply not grades but clades, and clades are monophyletic. These groupings are unlikely to be monophyletic. On the other hand, the simpler, sequential analysis is designed to test for monophylesis using the parsimony criterion and to do this using one putative sister taxon at a time.

Our rationale can best be explained by analogy to the use of the principle of parsimony as a methodological tool in nearly all cladistic analyses. Methodological use of the principle of parsimony does not mean that one believes that evolution is necessarily parsimonious but the method permits testing treelength against the parsimony criterion.

Parsimony can be used methodologically even though we think that sometimes evolution may not be parsimonious (Crisci 1982). In the same fashion we have employed parsimony as a criterion of monophyly. The shorter trees are more likely to be monophyletic than the longer trees. This is not to say that trees of groups that are not monophyletic must be longer than trees of monophyletic groups. We are using the principle of parsimony methodologically in order to gauge various trees of different evolutionary units.

We have no quarrel with Simpson's suggestion in principle, regarding global analyses or the substitution method (meaning to him the use of subsets of the total number of taxa). Such analyses should not be used blindly but rather when one already knows that the group or putative sister taxon itself constitutes a monophyletic group in combination with the study group. This often is not established and certainly was not in our situation.

We imagine that one response to our above explanation of why, in our particular case, global analysis or analysis of subsets of taxa are not reasonable approaches might be that something is wrong with the selection of putative sister taxa. We reemphasize that
we simply did not know which are the closest relatives of Bromeliaceae. This was one of our questions. We therefore tried various, likely monocot families sequentially and used parsimony to gauge which trees were most likely to represent monophyletic groups.

We made no prior assumptions about monophyly or polarity of the root of our ingroup except to note that the group of ten itself probably represents a grade not a clade nor did we need to assume monophyly about any subset of these ten. Regarding sister taxon status, results regardless of the outgroup, converged to implicate Bromeliioideae and Tillandsioideae as sister subfamilies.

As we noted previously, Simpson places enormous faith in global analysis. He points out that “...if the ‘true’ sister group (from the global analysis) shows a certain degree of convergence with a member of the ingroup” (increasing the apparent number of character state changes, i.e., reducing parsimony), then sister group designation from sequential analysis may be in error. This we feel to be a valid criticism of the parsimony method as applied not only to sequential analysis such as we used but equally to global analysis and analyses of subsets whatever the size of these subsets. Nevertheless, the parsimony method remains a powerful tool.

Simpson rightly notes that we have tended to look for congruences among trees. He goes on to say that a “...majority occurrence ... does not in itself argue that it is valid” and he cites Donoghue and Cantino (1984) as pointing out that certain congruences may occur simply because the outgroups (or putative sister taxa, see below) may be mostly very distantly related to the study group. We agree. However, this is not an effective argument against our particular results. Because of our own preliminary research and research of Dahlgren and Bremer (1985), Dahlgren and Clifford (1982), Dahlgren and Rasmussen (1983), as well as research of others, it is not true that most of our putative sister taxa are distantly related to the bromeliad subfamilies though some probably are so, e.g., Pandanaceae. Several lineages probably are represented and each is linked to Bromeliaceae to some degree, though less closely linked to one another (see our 1987 paper).

Simpson points out that if the hypothetical ancestor is extremely far removed from Bromeliaceae, its presence in the analysis may yield faulty information about character polarities and the topology of the ingroup. Lundberg rooting (see above) helps to circumvent this problem. Initially, ancestral states are ignored and the shortest network (unrooted tree) is found. Only then is the tree rooted by the outstates of the hypothetical ancestor thereby avoiding possible deleterious effects on the ingroup topology (see Meacham 1984; Swofford 1985). Results with Lundberg rooting did not differ from those in our 1987 paper, and thus were not mentioned.

The hypothetical ancestor is defined in Dahlgren et al. (1985, pp. 80–86). Relative to our dataset, we could score nine characters. The codes for the characters and states are as follows: 1(1), 4(1), 5(2), 6(1), 8(1), 9(2), 12((1), 18(2), 20(1)). The rationale for using the hypothetical monocot ancestor to root trees was explained in our paper. This allows the putative sister taxa to float and join with any one of the study group taxa (bromeliad subfamilies) if that happens to be the most parsimonious resolution just as occurred when Strelitziaaceae and Velloziaceae were used together.

Evolutionary Units and Characters. Simpson wonders about some of our choices of evolutionary units and our characters and character states. We welcome this opportunity to discuss these further here.

Strelitziaaceae were used rather than the ancestral states for the entire order Zingiberales as suggested by Simpson, because we wanted our evolutionary units to be as comparable as possible. That is, we tried to use representative families throughout and not orders here, and families there.

Simpson calls attention to character 4, stomates, character 14, cell wall of foliar scale, and character 15, scale development. It is true that these provide little information for resolving relationships but they do show character-state information that may be useful in the future. Therefore they were included. Certainly their presence as Simpson points out does not help to resolve relationships implied by the data matrix nor do they effect the cladistic analyses in any manner. The inclusion of character 8, endosperm, also does not alter the results or interpretations.

The two states of character 9, one or four nuclei, or two nuclei per tapetal cell, were established on the basis of what character combinations commonly occur within families. The same logic was used in selecting the character states for character 11, chromosome number. Character 17, ovary position was coded so that as little information as possible would be lost while still representing each taxon’s character information in as discrete a manner as possible. More discussion of this polymorphic character, such as Simpson provides, we realize, should have been included in our paper. The database for character 20, pollen type data, has been expanded on the basis of Simpson’s comments, in particular character 20 for Velloziaceae, which now reads 1 as per Simpson. We ran analyses again with this change and found that the sister taxon status of Bromeliioideae and Tillandsioideae remained unchanged.

Conclusions. Regarding the notion that global analysis provides the true resolution, we find no compelling theory or model that dictates that this is true. Perhaps this is someone’s canon, but we feel it is important to take a less doctrinaire and more eclectic approach. Certainly it depends upon the make up of the taxa that are included. There exists an a posteriori reason for not using global analysis with our data. If
reticulate evolution were a part of the evolutionary history that preceded the formation of the Bromeliaceae lineage (as we now think is true), then combining in a single cladistic analysis, two or more lineages that may have hybridized could lead to misidentification of actual synapomorphies as homoplasies (Humphries and Funk 1984).

In addition, because of the possibility of diploidization being manifested following paleo polyploid hybridization, two parents of a paleohybrid that are analyzed together with the study group may interfere with the recognition of true synapomorphies. This would be particularly likely if few new genes were expressed morphologically in the paleohybrid.

Simpson places too much faith in global analysis without consideration of the taxa being involved. The bromeliad analyses (based on the data set in our paper) reported by Simpson and those we report here (e.g., figs. 1 and 2) do not invalidate monophyly of the Bromeliaceae as Simpson states they do. Monophyly of Bromeliaceae is supported by a body of evidence that extends beyond the data in our data matrix.

It would have been nice to know beforehand "what is ancestral for the Bromeliaceae," but we did not know this. This was one of our questions which we were able to help answer by the research described in our paper. Outgroup substitution (one outgroup at a time, i.e., sequential analysis) was carried out and this 1) supported sister taxon status of Tillandsioideae and Bromelioideae, and 2) suggested Velloziaceae as very close and a good approximation of the sister taxon for the family. At the moment it seems unlikely that Velloziaceae is a part of the bromeliad lineage given the lack of identifiable uniquely derived traits supporting monophyly of this branch.

We agree with many of the points made by Simpson in the final paragraphs of his paper. In the future, more characters than we used should be examined and analyzed. Dahlgren and co-workers have set the stage. We hope that their research, that reported in our 1987 paper, and that discussed by Simpson will be followed by more work by other researchers.

We agree with Simpson that discussion of features used to characterize the bromeliad family are requisite to cladistic research. Discussion of bromeliad family traits is readily available. Such information can be found in the several works by Dahlgren and co-workers (cited in our paper and referred to by Simpson). Discussion is included in our own papers, and, of course, much information is available in the 2142 page monograph by Smith and Downs (1974, 1977, 1979). Nevertheless, the last word has not been heard. The unending synthesis (Constance 1964) endures. We agree also that identification of critical character-state changes, e.g., synapomorphies discussed in our paper, should constitute an important portion of any cladistic analysis.

We appreciate especially Simpson’s comments on future directions for research. We agree with his assessment that some of our characters need more research. As he puts it, some characters have a limited database in spite of excellent sources such as Dahlgren and co-workers. Only the way has been pointed out for future research.

Finally we wish to thank Simpson for his commentary and to point out that our paper and Simpson’s commentary (as we think he would agree) are illustrative of an advantage of the cladistic method over simply stating one’s conclusions as was often done for phylogenetic reconstruction before the advent of cladistics. In cladistics, just as with phenetics, the data used in an analysis are explicitly available and can be evaluated; the assumptions are stated, and the method of analysis is enunciated. Results and phylogenetic interpretations can be discussed more precisely with cladistic procedures than otherwise might be possible.

Last but not least, the results of phenetic and cladistic analyses can be compared as was done in our 1987 paper on the Bromeliaceae. The noted discrepancies were heuristic in helping to suggest to us a new interpretation, i.e., hypothesized paleohybridization between two or more monocot lineages being instrumental in founding the Bromeliaceae lineage.

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—Amy Jean Gilmartin, Marion Ownbey Herbarium and Department of Botany, Washington State University, Pullman, Washington 99164, and Gregory K. Brown, Department of Botany, University of Wyoming, Laramie, Wyoming 82071.