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COMPLEXITY AND HOMOLOGY IN PLANTS

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I. INTRODUCTION

Interest in phylogenetic analysis has focused attention on the concept of homology, especially on how hypotheses of homology are tested. Our object is not to review these developments (for which see Donoghue, 1992; also de Pinna, 1991; Haszprunar, 1992; Mindell, 1991; Minelli and Peruffo, 1991; Rieppel, 1988, 1992; Roth, 1991). Instead, we analyze factors that underlie the efficacy of proposed tests of homology and attempt to develop a general conceptual framework within which to consider homology and homoplasy in plants.

Our intention is not to promote a particular definition of homology, nor to propose a new one. Because our main interest is in phylogeny, our analysis is primarily a contribution to the *historical* view of homology, broadly understood (e.g., Hennig, 1966; Wiley, 1981; Patterson, 1982), as opposed to the *biological* view (e.g., Wagner, 1989a,b; Roth, 1988, 1991; also see Chapters 8, 9, and 13 in this volume). This is not to say, however, that synapomorphy or the history of character transformations are the only legitimate concerns connected with homology (Donoghue, 1992); as we will conclude, there are obvious connections between the two approaches.

II. BACKGROUND

The view is widespread that hypotheses of homology can be tested in various ways and that some tests are more powerful than others, in the sense that they are more effective in correctly identifying instances of homology. Patterson (1982), for example, outlined a series of homology tests for morphological features, and argued that the ultimate arbiter was what he called the *congruence test*. According to Patterson's "taxic" view of homology, a character is homologous if, and only if, it marks a monophyletic group. To test whether or not this is true, a character that is hypothesized to be homologous (having passed initial similarity tests) is included in a phylogenetic analysis along with other such characters. If the character is found to be a synapomorphy then it is considered

homologous. If it fails to mark a single clade, then the initial homology hypothesis is rejected and an instance of homoplasy is identified.

Patterson's (1988) analysis of homology in molecular characters led him to a different conclusion, namely that similarity is the more powerful test in this case than congruence. The reason, according to Patterson, is that it is possible to assess the probability that two molecular sequences could have achieved a certain level of similarity by chance alone. Thus, whether congruence or similarity is more powerful depends on the type of data under consideration.

We begin our analysis by taking a closer look at this view of the homology problem. Although we agree with Patterson that different tests may be more effective in different cases, we think this is not directly linked to whether characters are morphological or molecular. Instead, the critical factor, which Patterson and others before him had identified, is the relative complexity of the structures under consideration. We then bring this perspective to bear on the the value of different homology tests in plants, where much concern has centered on the supposed simplicity of plant structures and developmental systems.

III. MOLECULES AND MORPHOLOGY

Patterson's (1988) argument that similarity is the decisive test in the case of molecular data rests on an assumption about what is being homologized. He supposes that whole sequences are being compared in order to determine whether particular genes are homologous. In this case, owing to the linear, "one-dimensional" arrangement of elements (amino acids, nucleotides), it is possible to calculate the likelihood that two sequences are as similar as they are by chance alone (as opposed to reflecting common ancestry). In contrast, morphology has too many dimensions (at least three, or four, if ontogeny is included) to make such calculations feasible. In other words, the main difference that Patterson sees between morphology and molecules hinges on our ability or inability to make the appropriate probability calculations. The implication is that if we could devise methods to measure whether

morphological structures matched by chance alone, then similarity would become the more decisive test in morphology as well. In fact, considering the extra dimensions associated with many morphological features, it should, theoretically, be possible to make even stronger arguments about homology, based on similarity alone.

Patterson's (1988) view that there is a difference between morphology and molecules loses force when attention is shifted, as it often is in practice, to assessment of homology at particular sites in a sequence (following an alignment procedure). In this case all we know is that some taxa share, for example, a cytosine at a particular site, while others have a guanine; there is no obvious way to make the sorts of probability calculations that apply to whole sequences. This being the case, similarity can hardly be a decisive test of whether any particular nucleotide is truly a homology. Instead, similarity (e.g., the sharing of an adenine) simply "validates it as worthy of testing" in other ways, as Patterson (1988, p. 605) argued for morphology. Congruence is the obvious test in this case, but for a somewhat different reason than in morphology. Similarity is a weak test in morphology (and congruence necessary), according to Patterson (1988), because structures are so complex that it is difficult to quantify the likelihood of homology, whereas it is weak in the case of individual nucleotides because they are too simple.

The argument above lead us to conclude that which test is most decisive is not directly linked to whether the data are morphological or molecular. Instead, decisiveness seems to vary as a function of the ability to quantify the likelihood that sharing a certain level of similarity reflects common ancestry. Even within molecular data this ability varies depending on the level of the problem at hand; for example, whether whole sequences are being compared or just nucleotides at individual sites. The same is presumably also true within morphological data, since there is variation from simpler to more complex structures.

IV. SIMPLICITY AND COMPLEXITY

The argument above shifts attention away from morphology versus molecules toward a more general factor

underlying the decisiveness of different homology tests, namely the relative simplicity or complexity of the features under consideration. The notion of complexity is obviously problematical, but for our purposes it varies with the number of parts or possible correspondences, and with how irregularly the parts are arranged (McShea, 1991, 1992). As complexity in this sense increases it should be easier to weed out chance as an explanation for similarity. Whole molecular sequences happen to be complex enough for the use of statistical tests, but not so complex that it seems impossible to concoct appropriate measures. Exact measures may not yet be available for morphological characters, but the same general reasoning applies to them as well.

The relative complexity of structures figured prominently in earlier treatments of the homology problem (see Riedl, 1978). Perhaps most importantly, it is evident in Remane's (1952) division of homology criteria into "principal" and "auxiliary." Most comparative biologists are well acquainted with Remane's principal criteria — similarity in position (or topography), in special structure, and through transitional (or intermediate) forms. It is less well known that Remane equated the usefulness of these criteria with the degree of complexity. For example, in reference to the structural criterion he noted that "certainty increases with the degree of complication and of agreement in the structures compared" (in Riedl, 1978, p. 34).

Remane's three auxiliary criteria, which apply to simpler structures, are rarely mentioned. Riedl (1978, p. 36) translated these as follows:

(1) "Even simple structures can be regarded as homologous when they occur in a great number of adjacent species" (the *general conjunctional criterion*);

(2) "The probability of the homology of simple structures increases with the presence of other similarities, with the same distribution among closely similar species" (the *special conjunctional criterion*); and

(3) "The probability of the homology of features decreases with the commonness of occurrence of this feature among species which are certainly not related"(*the negative conjunctional criterion*).

While these are obviously not described in cladistic terms, they do rest squarely on the distribution of a feature in relation to other characters and on presumed phylogenetic relatedness, and therefore are similar in intent to Patterson's (1982) congruence test.

Patterson (1982), who made no mention of Remane, effectively elevated the criteria Remane intended as secondary, and for simple structures only, to his primary criterion for morphological characters (Donoghue, 1992). Many morphological characters can be evaluated using Remane's primary criteria, but Patterson (1988, p. 605) believes that these measures are too weak in morphology, which "has so far resisted quantification (and is unlikely to submit)." Thus, morphological characters are treated by Patterson as though they are simple structures — not because they really are — but because they are too complex to quantify.

We think it will clarify matters to reorient the discussion primarily around complexity, whether or not we happen to be able to perform the sorts of statistical tests that Patterson finds convincing. Under this view, complex morphological features and whole molecular sequences (both of which allow many comparisons) are situated at one end of the spectrum, where similarity can provide a more powerful preliminary test. Simple morphological structures and individual nucleotide sites are located near the other end of the continuum, where there is little else to go on but congruence with other evidence.

V. COMPLEXITY AND HOMOPLASY

It is important to remember that we are concerned here with the power of similarity tests to identify truly homologous features at the outset, before phylogenetic analysis. Because homology (at least "historical" homology) is tied to inheritance from a common ancestor, congruence testing is always necessary (de Pinna, 1991). That is, no matter how complex the structures involved, or how powerful the similarity tests may therefore be, phylogenetic analysis has at least the potential to favor homoplasy over homology. The significance of our arguments above is that they lead to a simple prediction. If the power of similarity to

correctly identify homology before phylogenetic analysis varies with character complexity, then fewer instances of nonhomology should make it past the similarity filter when greater complexity makes the filter that much finer. That is, there should be fewer instances of homoplasy identified in phylogenetic analysis in the case of complex characters. This, we note, is similar to (though far less extreme than) some arguments underlying Dollo's Law (see Sanderson, 1993). On the other hand, when the filter is necessarily coarse, as in the case of simple structures, we should expect to see more homoplasy. These expectations are illustrated in Fig. 1.

Fig. 1. Expected relationship between the relative complexity of characters, the stringency of the similarity tests applied, and levels of homoplasy observed in phylogenetic analysis. A group of less complex characters (group 1 on the lower left, each character represented by a small cross-hatched rectangle) is necessarily subjected to limited similarity tests (dotted lines connect individual characters through different levels in the diagram). Note that complexity and strength of similarity test both increase to the right. Although the range of retention index (RI) values is great (some characters showing little or no homoplasy), the average level of homoplasy is relatively high. Note that the amount of homoplasy decreases to the right. The shaded curve above represents a histogram of RI values for a hypothetical large population of simple characters. In contrast, the group of more complex characters (group 2 on the lower right, represented by black rectangles) is subjected to more stringent similarity tests. On average, these characters show less homoplasy than characters of type 1. The open curve is a histogram of RI values for a large population of complex characters. The mean RI values of the two populations of characters are widely separated, although the distributions overlap.

This prediction relating complexity to homoplasy is at least potentially testable using phylogenetic studies. But is it really worth testing? We think that it is for two reasons. First, it need not be true. For example, the level of homoplasy shown by different characters might track some

other factor, which may or may not covary with complexity, such as the degree of *burden* or *entrenchment* in development (Riedl, 1978; Arthur, 1988; Wimsatt and Schank, 1988). A character that is peripheral in development and of low burden might otherwise be complex in the sense of being elaborate and amenable to numerous point comparisons (e.g., the lip petal in orchid flowers). Second, attempting to test such a prediction using phylogenies will help us better understand the logic and limitations of such tests; that is, how much we can expect to learn from trees about general patterns of character evolution.

What would a proper test require? First, one would need to be able to categorize characters at the outset as to their complexity (see below). Second, phylogenies would be needed to compare levels of homoplasy in characters recognized as more and less complex. Indirectly, the proposition has perhaps already been tested in our comparison of levels of homoplasy in morphological versus molecular phylogenetic studies (Sanderson and Donoghue, 1989; also see Donoghue and Sanderson, 1992). If we could safely assume that morphological characters were prescreened by more powerful similarity tests than simpler molecular characters, we would expect to see more homoplasy in molecular data. We found, however, that there was not a significant difference between the two sorts of data. This may mean that our prediction was incorrect, but interpretation of the results is difficult. For example, there may be less prescreening of morphological characters than their complexity would allow, or there may be more prescreening of molecular characters (e.g., by elimination of segments of DNA showing ambiguity in alignment).

Givnish and Sytsma (1992) extended this kind of analysis to a comparison of chloroplast DNA restriction-site data, nucleotide sequence data, and morphology in plants. They reported significantly less homoplasy in restriction-site analyses, which they interpreted to mean that such data "provide an internally more consistent basis for phylogenetic studies" (Givnish and Sytsma, 1992, p. 145). This is either tautologically true or they meant to imply that restriction-site data yield a more reliable estimate of relationships. As we demonstrated previously (Sanderson and Donoghue, 1989; Donoghue and Sanderson, 1992)

there does not appear to be a direct link between consistency index and reliability, but it is nevertheless worth considering what might account for the observed pattern. In view of the inability to distinguish among different mutations that could lead to loss or gain of a restriction site, it is likely that some homoplasy is simply hidden. Of course, this implies that taxa in such studies are sometimes united by false synapomorphies. Another possibility is that the general pattern results from more stringent screening of restriction-site data, perhaps through omission of bands that are not easily mapped. Alternatively, Givnish and Sytsma's (1992) result may reflect some other variable that was not taken into account. In this case, we suspect that differences in the level of resolution of phylogenetic relationships need to be considered. Trees based on restriction-site data may tend to show more unresolved regions owing to lack of evidence, in which case the effective number of taxa in such studies is reduced.

de Queiroz and Wimberger (1993) used a similar approach to compare behavioral and morphological characters, and concluded that there is not a significant difference in the level of homoplasy between the two. If, as is sometimes said (see de Queiroz and Wimberger, 1993), behavioral characters are subject to a limited set of similarity tests (e.g., the positional criterion might be inapplicable), then more homoplasy would be expected in the behavioral traits. That this is not observed suggests that similarity tests are actually as stringent in behavior or that less intense tests are not resulting in more mistakes in identifying homology.

VI. HOMOLOGY AND HOMOPLASY IN PLANTS

How is an expected relationship between complexity and homoplasy relevant to the homology problem in plants? The connection is that botanists have been skeptical about homology assessment in large part because plants are seen to be structurally and developmentally simpler than animals. Stebbins (1974), for example, echoes the standard view that owing to "relative indeterminism with respect to both the number and the position of plant parts, these criteria are much less diagnostic of homology in plants than in animals"

(p. 142). He goes on to say that "developmental pattern is also a much less reliable criterion of homology in plants than in animals," because "patterns of development of individual organs are, in general, much simpler in plants than in animals" (p. 143). For these reasons plant morphologists have tended to shy away from the evolutionary connotations of homology, opting instead to define it in terms of similarity alone (e.g., Sattler, 1984; Kaplan, 1984; Tomlinson, 1984; but see Stevens, 1984).

Skepticism on the part of botanists is quite understandable when one lists the relevant differences between plants and animals (see Klekowski, 1988, p. 170). Plants have probably only one-tenth to one-twentieth the number of cell types, and these are distinguished mainly by the nature of the cell wall, since cell movement (as is an immune system) is basically lacking. Furthermore, plant cells tend to be totipotent and show greater plasticity than animal cells. Owing to indeterminate growth (a distinct germline is absent) and modular organization, developmental steps are generally repeated many times in different parts of the plant. Iterative (serial) homology promotes the possibility of something analogous to the paralogy problem in multigene families (Roth, 1991, and Chapter 10 in this volume). Moreover, plants may be especially prone to processes that disrupt the usual correlations seen in animals (especially vertebrates); for example, homeotic or heterotopic events that shift the position of a feature but not its structure or ontogeny (Iltis, 1983; Meyen, 1988; Sattler, 1988).

Along these same lines, Kaplan (1992) has pointed out that a fundamental distinction between multicellular construction in plants and animals stems from an underlying difference in cell division. In animals there is complete separation of protoplasts at mitosis, whereas in plants incomplete separation results from the insertion of walls with plasmodesmata. Kaplan argues that the application of an animal-biased cell theory has resulted in an inappropriate emphasis on structural qualities as a guide to homology in plants. He promotes, instead, an "organismal theory," which emphasizes positional criteria.

These observations, coupled with our arguments above, imply that similarity tests in plants might be less able to weed out nonhomology at the outset, and that plant data

sets might therefore show more homoplasy than animal data sets. This difference was not observed in our earlier comparsions (Sanderson and Donoghue, 1989). In fact, we found remarkably similar levels of homoplasy in plant and animal phylogenetic studies, and we suggested that this might reflect a tendency for botanists to simply disregard more characters at the outset than zoologists. Another possible explanation is that there truly is more homoplasy in the characters included by botanists, but that phylogenies provide an underestimate because they are either false or not finely enough resolved. A third, more optimistic, explanation is that despite the relative simplicity of plant structures and development, botanists are nevertheless able to distinguish homology from nonhomology just about as effectively as zoologists.

It is difficult to choose among these possibilities, which, of course, are not mutually exclusive. The first proposition is difficult to test given the usual inattention to rejected characters. Although we are tempted to accept the third explanation, the second one remains a distinct possibility. After all, it is quite often the case that taxa added to an analysis will be positioned so as to require additional homoplasy. This is true in general (Sanderson and Donoghue, 1989) and there are many concrete examples in plants, even involving the most complex structures. Good examples are the evolution of roots and leaves in land plant sporophytes. Analysis of living plants alone implies that these organs evolved just once — that they are synapomorphies of trachaeophytes. However, analyses including fossils suggest that both organs evolved within the zosterophyte/lycophyte line and again within the trimerophyte line (e.g., Kenrick and Crane, 1991). Likewise, without "progymnosperm" fossils one would suppose that fern leaves and seed plant leaves were homologous (Doyle and Donoghue, 1986; Donoghue *et al.* 1989). It has not been difficult for some botanists to conclude that if we had an accurate enough phylogeny, every plant character would be seen to have evolve more than once — real synapomorphies are an illusion and parallelism must be used to infer relationships (e.g., Cronquist, 1988). Of course, a better understanding of phylogeny can also decrease homoplasy in some characters. An example is the recognition that double

fertilization may be homologous in gnetales and angiosperms (see Donoghue and Scheiner, 1992).

VII. A POSSIBLE TEST

From the preceding discussion it should be clear that more direct tests are needed, designed to eliminate (or minimize) at least some of the possibly confounding variables noted above. In this spirit we have conducted a preliminary comparison of plant characters that are often viewed as being more and less complex. Although in some respects this is an improvement over the broad comparisons discussed above, it is clearly still far from ideal. Nevertheless, we think studies along these lines warrant further attention. If nothing else, they clarify what we can expect to extract from such comparisons.

Our aim was to select from the literature a set of plant phylogenetic studies containing morphological characters of varying complexity that could be compared among studies. Ideally, one would apply a specific measure of complexity to all of the characters in a number of data sets and then compare levels of homoplasy among complexity classes. Although some attempts have been made to quantify complexity (e.g., Schopf *et al.*, 1975; Riedl, 1978; Bonner, 1988; McShea, 1991), we know of no measures that can readily be applied to the range of morphological characters encountered in phylogenetic data sets.

Schopf and colleagues (1975) judged the complexity of organisms by the number of terms used to describe them. This suggests the possibility of quantifying the complexity of individual characters by counting the number of descriptive terms (or leads in a diagnostic key) associated with particular features. However, it is not clear to us that there is a straightforward relationship between number of descriptors and complexity. For example, although there are many terms describing pubescence in plants, botanists tend to regard hair characters as being relatively simple. Another problem is that it is unclear what phylogenetic universe to consider in counting numbers of character states. Should the number of terms be tallied for all green plants, all seed plants, all angiosperms, or perhaps only for the data sets under consideration? Bonner (1988) concentrated on the

number of cell types, a measure more easily applied in broader comparisons (such as between green plants and vertebrates) than within angiosperms, especially in view of the presence in many plant structures of the same basic cell types (see above). McShea's (1992) metric uses a series of single measurements on a set of serially homologous structures, and therefore is inapplicable to most of the characters in cladistic data sets.

In view of these difficulties, we opted instead to make preliminary comparisons among sets of characters that have traditionally been viewed as more and less complex, and therefore more and less likely to provide an accurate guide to phylogeny. Furthermore, rather than attempting to categorize all characters in each data sets, we decided to focus on just a few contrasts. Initially we compared pubescence/trichome characters with flower characters (excluding pubescence, inflorescence, and fruit characters). A third class was added later, comprised of all leaf characters except pubescence and phyllotaxy. The fact that these different character types were present within the individual studies helps factor out differences between systematists in the choice and coding of characters. It also guards against artifacts that might arise if certain classes of characters were mostly used in studies at higher taxonomic levels (greater phylogenetic depth) and others at lower levels.

Regarding complexity and expected homoplasy in these three classes, we believe it is fair to say that botanists have generally considered flower characters to be more complex and more reliable, on average, than either pubescence or leaf characters. This view is expressed with little reservation in some older texts (e.g., Jeffrey, 1917), whereas in more recent discussions counter examples are usually offered to illustrate that characters of all kinds can be phylogenetically useful (e.g., Davis and Heywood, 1973; Stace, 1989; on leaves in particular, see Levin, 1986; Hershkovitz, 1993). Nevertheless, even recent treatments imply that, on average, flower characters tend to be most useful. Stebbins (1974, p. 152), for example, developed an argument similar to ours, namely that "the degree of irreversibility of a character condition depends upon the number and complexity of the separate factors that contribute to it." On this basis he concluded (pp. 148-151)

that more reversibility is to be expected in characters having to do with size (e.g., leaf size) and amount (e.g., pubescence) than those reflecting the fusion and adnation of flower parts or differences in flower symmetry. In general, Stebbins (1974) adopted what we believe to be the standard view, namely that vegetative characters are more plastic and more prone to convergence and parallelism (e.g., pp. 43 and 49), whereas flower characters are more complex and therefore more conservative (e.g., pp. 100 and 125).

In selecting data sets from the literature we used the database of Sanderson *et al.* (1993) to locate 85 morphological cladistic analyses of angiosperm groups published from 1989 through 1991. These studies were scanned for data matrices that included both trichome and flower characters, and 10 were selected for further analysis (Table I). Each of these data sets was then reanalyzed, using Phylogenetic Analysis Using Parsimony (PAUP, version. 3.0s; Swofford, 1991). In most cases we were able to confirm the phylogenetic results presented in the original paper, but in a few cases (Anderberg and Bremer, 1991; Kron and Judd, 1990) we found additional most parsimonious trees, or (Cox and Urbatsch, 1990) even slightly more parsimonious trees. Insufficient information was given in two of the papers (Cruden, 1991; Loconte and Estes, 1989) to ascertain whether our results exactly matched those presented.

MacClade (version. 3.0; Maddison and Maddison, 1992) was used to parsimoniously optimize the selected characters on the trees obtained and to calculate the consistency index (CI) and retention index (RI) for each character, as well as ensemble CIs and RIs for suites of characters (see Table I). Because the RI is undefined (0/0) for autapomorphies, these were excluded in calculating this measure. Our attention will focus on RI comparisons, because we think this is the more appropriate statistic in this instance. The CI is affected by the distribution of character states among the taxa, whereas the stringency of similarity tests is probably independent of the number of taxa with alternative states. Where more than one most parsimonious tree was found, MacClade was used to calculate average CI and RI values over the entire set of most parsimonious trees. While this procedure effectively weights each tree equally, it is unlikely that this would bias the results and, in any case, it seems preferable to examining only a single tree.

The number of characters of the three types *within* the individual studies is so limited (Table I) that we cannot draw strong conclusions from such comparisons. For example, flower RIs exceeded pubescence RIs in six studies, pubescence RIs were higher in three, and the two were tied in one data set. Flower RIs were higher than leaf RIs in three cases, leaves were higher in three, and flowers and leaves were tied in the remaining two. None of the possible contrasts between character types was found to be significant on the basis of a nonparametric Wilcoxon signed-rank test.

Failure to find a significant difference between character types within data sets led us to pool characters from the 10 studies to increase sample sizes (Table I). The average RI is 0.63 for the 18 pubescence characters, 0.71 for the 21 leaf characters, and 0.77 for the 66 flower characters (RI calculations are based on fewer characters than shown in Table I because autapomorphies were omitted). These values are consistent with our prediction, but statistical tests (t tests and nonparametric Mann-Whitney tests) for differences among pooled character classes, as well as between vegetative characters (pubescence plus leaf characters) and flower characters, revealed no significant contrasts (although the difference between pubescence and flower RIs came closest to being significant). There may be differences in the variance of RIs among the character types, but the data are still too limited to assess this possibility. The histogram of flower RIs is skewed right, with an excess of RI = 1 and a deficit of RI = 0 characters, whereas the distribution of pubescence RIs is almost uniform from 0 to 1.

Although pooling characters increases the sample size, it also introduces a possibly confounding variable. The number of taxa included in the individual studies ranged from 11 to 44, and it is known that, on average, there is a positive correlation between the number of taxa and the amount of homoplasy, at least as measured by CI (Archie, 1989; Sanderson and Donoghue, 1989). The absolute values of CI obtained would presumably be highly influenced by the distribution of study sizes. It is unclear, however, that differences in study size would introduce a systematic error in the comparsions we have made between character classes, unless there also happens to be a correlation

between the number of taxa and the number of characters of each type in the study (e.g., if the larger studies accounted for most of the pubescence characters). Ideally, one would compare studies that include approximately the same number of taxa; however, we found it was difficult enough to locate a reasonable number of studies of any size with the right kinds of characters.

These results imply that there is little difference among the character classes in levels of homoplasy. RI comparisons across data sets do suggest a tendency for pubescence (and perhaps leaf characters) to show more homoplasy than flower characters, as predicted. However, on the basis of the present analysis we cannot conclude that this is a significant difference. Our intention is to extend this analysis to more data sets to see if a clearer pattern emerges as we increase the sample size. In the meantime, it is instructive to consider possible reasons why we do not see stronger support for the predicted pattern. One possibility, of course, is that there is something fundamentally wrong with the prediction. However, before abandoning the hypothesized connection between complexity and homoplasy it will be necessary to address several limitations of the present analysis.

Perhaps the least reliable assumption of our analysis is that the character categories we established at the outset really do correspond, on average, to differences in complexity. It might be the case, as shown in Fig. 2, that within each of these categories there is such a range of variation in complexity that the expected pattern between classes is obscured. That is, the classes we delimited, which we hoped would be distinct, are really overlapping. Our results might simply be an argument against the standard intuition about levels of homoplasy in such classes — flower characters, taken collectively, show no less homoplasy than leaf or pubescence characters.

Fig. 2. Factors that may contribute to a failure to observe significant differences in homoplasy between character types. All symbols are described in Fig. 1. In contrast to the expectation shown in Fig. 1, a greater range of variation in complexity exists within each set of

characters (groups 1 and 2), such that their ranges broadly overlap. Also in contrast to Fig. 1, the more complex characters are not subjected to as strong a similarity test as they could be (i.e., the black rectangles are generally shifted to the left on the axis representing the strength of similarity test). The net effect of these differences is that homoplasy levels in the two sets of characters become more broadly overlapping, and the mean RIs more similar. Under these circumstances greater sample sizes would be needed to detect a significant difference.

Another possibility, also shown in Fig. 2, is that there are average difference in complexity among the classes we have defined, but that these real differences are not well reflected in the actual scoring of characters for phylogenetic analysis. First, the process of prescreening characters in assembling a data matrix may tend to eliminate the very simplest morphological characters, and this might have the effect of bluring differences between character classes. Second, just because a character is potentially complex, and therefore potentially subject to stringent similarity tests, does not guarantee that such tests were actually performed. In other words, systematists may not be taking full advantage of the possibility of more detailed similarity comparisons. Instead, they may be performing about the same, relatively low, level of similarity testing regardless of the underlying complexity of different characters. In Fig. 2 this is illustrated as a general shift toward less stringent similarity tests for the more complex characters than shown in Fig. 1.

We suspect that if morphological structures were compared in greater detail (for example, by taking into account development) clearer differences among classes of characters might then emerge. A good example concerns sympetaly, or the union of petals into a floral tube. It has often been assumed that the vast majority of sympetalous dicots are related, and these are commonly united as Asteridae (e.g., Cronquist, 1988). However, phylogenies based on the chloroplast gene *rbc*L imply that there are several separate clades of "Asteridae" and that sympetaly must therefore be homoplastic (Donoghue *et al.*, 1992; Olmstead *et al.*, 1992). Recent developmental studies by Erbar (1991) have shown that there are at least two distinct

developmental systems underlying sympetaly, and these appear to delimit groups that are congruent with clades, based on molecular evidence. The point is that a more detailed analysis of "sympetaly" at the outset, taking advantage of the potential to perform a more stringent similarity test using ontogenetic information, would have led to the recognition of distinct states and, consequently, to a reduction in homoplasy. The same may also be true of such characters as "roots" (Bierhorst, 1971; Groff and Kaplan, 1988).

The two factors just discussed could be working together to blur the expected relationship between complexity and homoplasy. The net result is that the two RI distributions are largely overlapping and the means are much closer together than they are in Fig. 1. It may be possible to establish a significant difference between classes even under these unfavorable circumstances, but it is clear that this will require much larger sample sizes.

More general problems with phylogenetic inference methods could also have influenced the outcome of our analysis. Basing conclusions about patterns of character evolution on trees derived in part from those same characters runs a risk of circularity. This risk may be low when a small subset of characters is of interest, as these might bias the outcome only slightly, but some of our contrasts (e.g., studies 1 and 7 in Table I) involved a sizable portion of the characters used to reconstruct the phylogeny. Circularity is only an issue, however, when the data suggest an erroneous phylogeny. If the phylogeny is correctly reconstructed it does not matter that the same characters are being subjected to further analysis, and the best estimate of phylogeny may be obtained when all of the relevant data are considered (Donoghue and Sanderson, 1992). In principle, tests of robustness can be used to eliminate results based on weak or highly conflicting data. The only troublesome cases would then be results that are robust but false, which are probably obtained only under a rather limited set of conditions (e.g., Felsenstein, 1978). One such set of conditions is when an entire suite of functionally correlated characters has arisen several times, but, by sheer weight of numbers, these characters lead to an erroneous reconstruction suggesting a single origin. If that suite happens to correspond to one of the character classes

involved in a contrast, then that class would have a misleadingly high retention index. However, this problem may be self-limiting inasmuch as it is unlikely that all the characters in an increasingly large subset of the data will be tightly correlated.

VIII. GENERAL DISCUSSION

The outlook we have developed can be viewed as an extension of Patterson's (1988) argument that the various homology tests are more or less powerful depending on the data under consideration. However, whereas Patterson saw a fundamental distinction between morphological characters (where congruence is primary) and molecular data (where similarity is decisive), we see the power of similarity tests varying as a function of the complexity of characters, of whatever type.

It is important to understand exactly where the difference arises between our outlook and Patterson's. It has nothing to do with the definition of homology, since we certainly agree that we want to identify characters that truly mark monophyletic groups. Nor is there disagreement over the types of homology tests (similarity, congruence, etc.). The difference is a more subtle one, which revolves around how the tests themselves are viewed as bearing on the evaluation of homology.

Patterson adopts the view that one or the other test will be the ultimate arbiter, depending on the type of data. He sees similarity tests as being so weak in the case of morphology that virtually the entire decision rests on congruence. In molecular data he sees similarity as such a strong test that congruence is superfluous. In any case, an hypothesis of homology is accepted or rejected on the basis of whether the decisive test is passed or failed.

In contrast, we see the power of similarity and congruence tests as varying more or less continuously, depending on the circumstances. Similarity tests are more likely to result in recognition of truly homologous structures when many points of correspondence are available for comparison. However, we would not conclude on the basis of similarity alone that structures are homologous (even in the case of molecular sequences). A congruence test is

needed in all cases to evaluate whether a character evolved only once or more than once (de Pinna, 1991). However, congruence tests also vary more or less continuously in power, depending on the character analysis preceding the analysis and on the strength of support for relationships (Mindell, 1991). In some cases a phylogenetic conclusion will be strongly supported and in other cases only weakly so. Confidence in such conclusions varies.

Our outlook certainly does not entail the acceptance of *partial homology* (e.g., Sattler, 1984; see Donoghue, 1992, and Chapter 13 in this volume). Homology itself is generally (and appropriately, we think) viewed as an all-or-none proposition, in the sense that a character either is or is not homologous in a particular group. Our discussion concerns the bearing of homology tests on hypotheses of homology, and it is the outcome of these tests that we see as varying quantitatively, as opposed to qualitatively (i.e., accept or reject; see Mindell, 1991). The strength of a particular homology hypothesis is a complex function of the stringency of the various tests that have been applied. On one end of the spectrum are hypotheses supported (or rejected) on the basis of limited similarity tests and a weak phylogenetic hypothesis. An example would be a shared nucleotide at a site (character) identified on the basis of dubious sequence alignment, which also happens to be only weakly supported as a synapomorphy by other characters in the data set. Near the other end of the continuum are hypotheses based both on stringent similarity tests and a strong phylogenetic hypothesis; for example, a complex morphological character whose status as a synapomorphy is supported by many other characters. Most cases, of course, lie somewhere between these extremes.

The significance of this difference in outlook is that the view we have developed leads naturally to the sort of prediction illustrated in Fig. 1, namely that congruence testing should uncover different levels of homoplasy depending on differences in complexity and the strength of similarity tests. As we have seen, phylogenetic tests of this proposition are problematical. The main stumbling block is that we have not found a way to readily evaluate complexity, and instead have had to resort to using proxies based on standard intuition (molecules versus morphology, plants versus animals, and now trichomes versus flowers). As a

consequence, our failure to find a clear difference among character classes might only indicate that those intuitions are misguided, rather than something more fundamental about evolution. In view of the compromises involved, and the variety of confounding factors discussed above, we are led to the general conclusion that tree-based studies aimed at discovering general patterns of character evolution will often require large sample sizes. Such studies will be greatly facilitated by the establishment of a database of phylogenetic evidence and trees (Sanderson *et al*, 1993).

The view we have developed helps put botanical skepticism about homology in perspective and leads to some concrete suggestions for improving the situation. Concern that the relative simplicity of plants renders similarity less reliable seems well founded in theory, but there is not a strong indication that botanists are making more mistakes about homology than zoologists. On the other hand, we suspect that botanists could do even better by taking advantage of opportunities to add dimensions to their similarity comparisons. One way to do this is to add developmental information, as in the sympetaly example (for other possibilities see Tucker, 1988; Endress, 1990; Hufford, 1990). Another very real possibility is to add information on the molecular basis of characters. This has become feasible with recent advances in understanding the genetics of flower development in *Arabidopisis* and *Antirrhinum*, and the availability of probes for some of the relevant genes (Coen and Meyerowitz, 1991). Another problem that could be addressed in this way is the homology of self-incompatibility systems in angiosperms (Weller *et al.*, 1993). Using molecular information (see Haring *et al.*, 1990) on *S* alleles in *Brassica* (with a sporophytic system) and *Nicotiana* (with a gametophytic system) to assess the location and sequence of *S* alleles in other taxa would provide the opportunity for a much finer resolution than is possible, based only on scoring the presence or absence of self-compatibility.

Finally, we note that our analysis hinges on the assumption that some characters are truly more complex than others. Although this may seem reasonable, it is difficult to establish because we lack a clear concept of "character" (Fristrup, 1992) and we lack appropriate methods for quantifying complexity (McShea, 1991). These

basic issues bring us directly to the work of Riedl (1978), Roth (1988, 1991), Wagner (1989a,b), (and see Chapters 8 and 9 in this volume) and others, who have tried to identify factors that promote the individuation of characters and the developmental phenomena that may maintain characters of differing complexity, such as hierarchical and cyclical ontogenetic networks. This, we think, is a critical and exceptionally promising intersection between historical and "biological" approaches to homology.

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TABLE I. Summary statistics on ten numerical cladistic analyses of Angiosperms and Levels of Homoplasy in Subsets of Characters.[a]

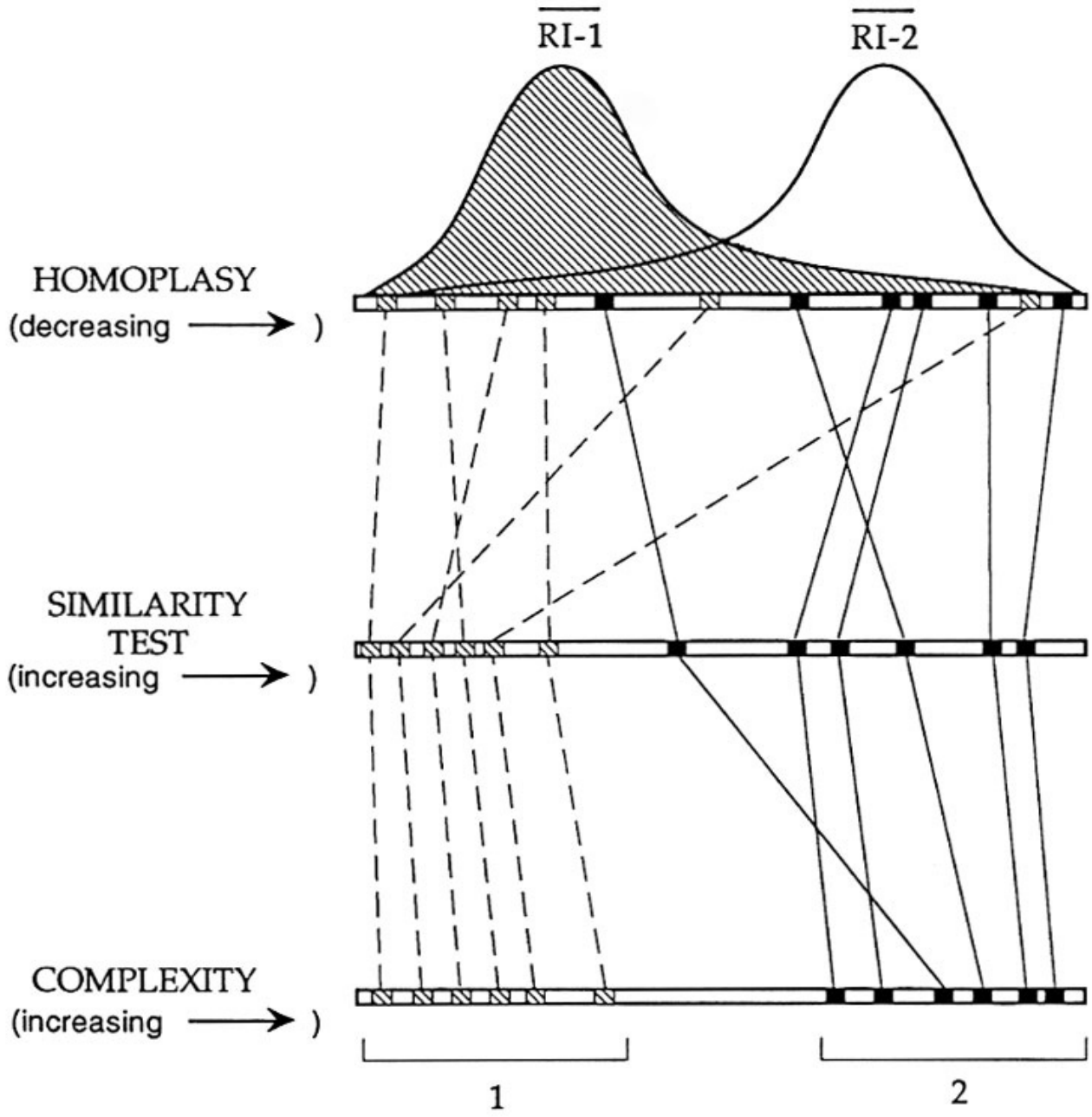
Study[b]	Taxa	Chars	Trees	Steps	CI	RI	No. Chars.			CI			RI		
							P	L	F	P	L	F	P	L	F
1	44	46	503	123	0.45	0.78	1	5	12	0.33	0.66	0.69	0.83	0.83	0.83
2	30	27	1	56	0.62	0.83	3	1	6	0.83	1.00	0.78	0.75	1.00	0.94
3	15	22	18	32	0.75	0.86	5	2	5	0.88	0.75	0.90	0.79	0.50	0.75
4	14	28	16	72	0.46	0.61	1	1	6	0.40	0.48	0.79	0.50	0.72	0.76
5	11	36	2	71	0.87	0.85	2	0	9	0.77	--	0.86	0.44	--	0.81
6	11	20	1	36	0.54	0.24	3	0	7	0.67	--	0.93	0.25	--	0.87
7	17	42	54	48	0.81	0.86	3	2	23	0.89	1.00	0.77	0.66	1.00	0.64
8	13	14	6	21	0.67	0.67	2	3	3	0.75	0.58	0.77	0.50	0.69	0.33
9	11	27	2	45	0.64	0.75	3	4	7	0.83	0.68	0.70	0.92	0.28	0.70
10	35	49	149+	124	0.48	0.78	1	4	10	0.17	0.71	0.49	0.50	0.78	0.78
Totals:							24	22	88	0.75	0.71	0.76	0.63	0.71	0.77

[a] CI, consistency index; RI, retention index; P, pubescence characters; L, leaf characters; F, flower characters.

[b] Studies: (1) Anderberg and Bremer, 1991: *Relhania* group (Asteraceae: Gnaphalieae); (2) Axelius, 1990: *Xanthophytum* (Rubiaceae); (3) Boufford, *et al.*, 1990: *Circaea* (Onagraceae); (4) Cox and Urbatsch, 1990: coneflower genera (Asteraceae: Heliantheae); (5) Cruden, 1991: *Isidrogalvia* (Liliaceae); (6) Gilmartin, *et al.*, 1989: *Glomeropitcairnia* (Bromeliaceae); (7) Judd, 1989: Miconieae (Melastomataceae); (8) Kron and Judd, 1990: Rhodoreae (Ericaceae); (9) Lavin, 1990: *Sphinctospermum* (Leguminoseae); (10) Loconte and Estes, 1989: Berberidaceae and Ranunculales.

The consistency index (CI) for a single character is m/s, where m is the minimum number of steps a character can show on any tree, and s is the minimum number of steps required on the tree under consideration. The ensemble CI for a suite of characters is M/S, where M and S are sums of m and s over all characters in the suite. The retention index (RI) for a single character is $(g - s)/(g - m)$, where m and s are as above, and g is the maximum number of steps that a character could require on any tree. The ensemble RI is analogous to the ensemble CI. For additional information see Farris (1989), Swofford (1991), and Maddison and Maddison (1992).

Figure 2. Factors that may contribute to a failure to observe significant differences in homoplasy between character types. All symbols are described in Figure 1. In contrast to the expectation shown in Figure 1, a greater range of variation in complexity exists within each set of characters (groups 1 and 2), such that their ranges broadly overlap. Also in contrast to Figure 1, the more complex characters are not subjected to as strong a similarity test as they could be (i.e., the black rectangles are generally shifted to the left on the axis representing the strength of similarity test). The net effect of these differences is that homoplasy levels in the two sets of characters become more broadly overlapping, and the mean RI's more similar. Under these circumstances greater sample sizes would be needed to detect a significant difference.


RI-1
RI-2
HOMOPLASY
(decreasing ⟶)
SIMILARITY
TEST
(increasing ⟶)
COMPLEXITY
(increasing ⟶)
1
2

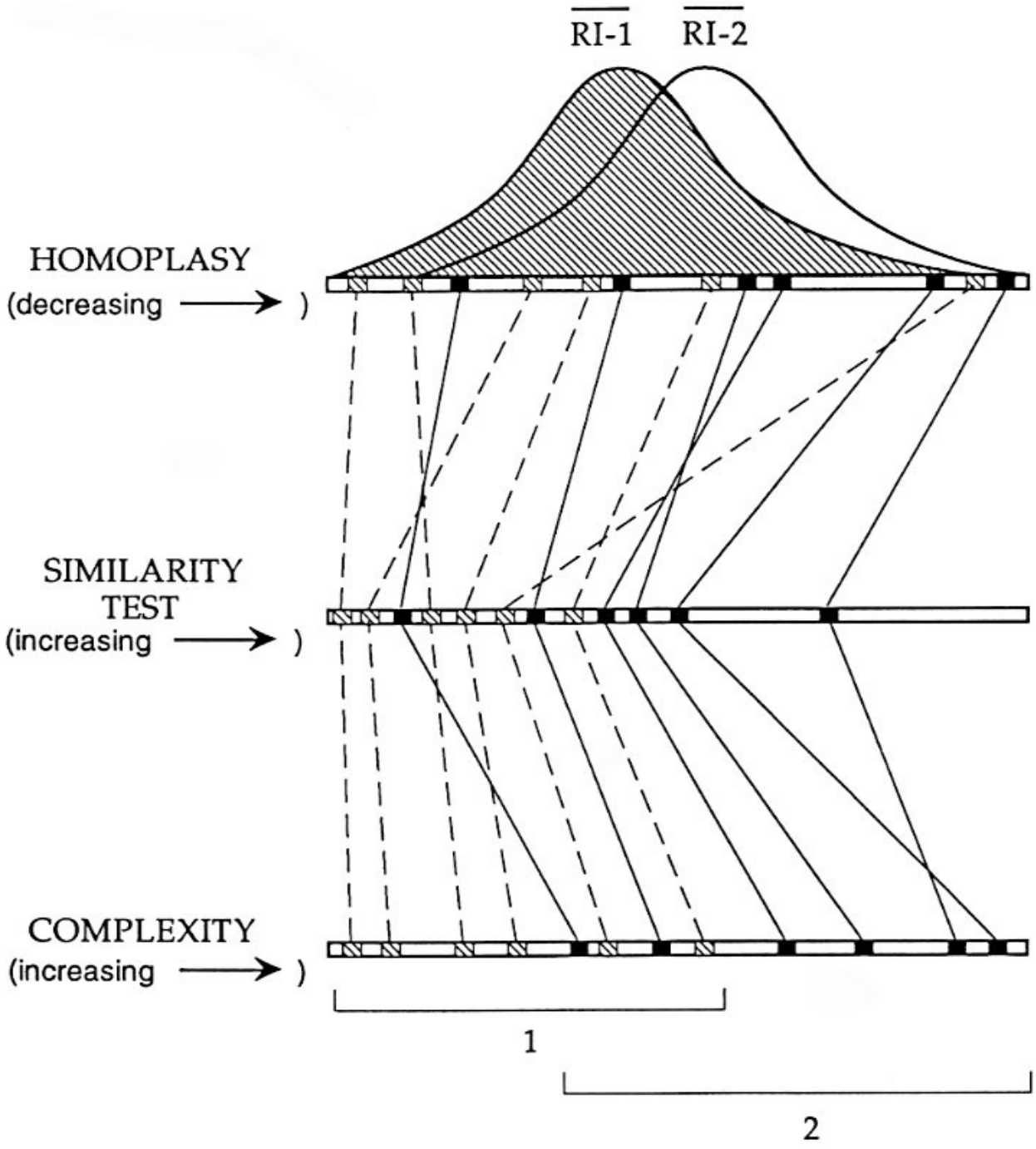

RI-1
RI-2
HOMOPLASY
(decreasing →)
SIMILARITY
TEST
(increasing →)
COMPLEXITY
(increasing →)
1
2

FIGURE 2

TABLE 1. Summary statistics on ten numerical cladistic analyses of angiosperms[1] and levels of homoplasy in subsets of characters: P = pubescence characters; L = leaf characters; F = flower characters; CI = consistency index[2]; RI = retention index[2].

Study[1]	Taxa	Chars	Trees	Steps	CI	RI	No.Chars.			CI			RI		
							P	L	F	P	L	F	P	L	F
1	44	46	503	123	.45	.78	1	5	12	.33	.66	.69	.83	.83	.83
2	30	27	1	56	.62	.83	3	1	6	.83	1.00	.78	.75	1.00	.94
3	15	22	18	32	.75	.86	5	2	5	.88	.75	.90	.79	.50	.75
4	14	28	16	72	.46	.61	1	1	6	.40	.48	.79	.50	.72	.76
5	11	36	2	71	.87	.85	2	0	9	.77	--	.86	.44	--	.81
6	11	20	1	36	.54	.24	3	0	7	.67	--	.93	.25	--	.87
7	17	42	54	48	.81	.86	3	2	23	.89	1.00	.77	.66	1.00	.64
8	13	14	6	21	.67	.67	2	3	3	.75	.58	.77	.50	.69	.33
9	11	27	2	45	.64	.75	3	4	7	.83	.68	.70	.92	.28	.70
10	35	49	149+	124	.48	.78	1	4	10	.17	.71	.49	.50	.78	.78
TOTALS							24	22	88	.75	.71	.76	.63	.71	.77

[1](1) Anderberg and Bremer, 1991: Relhania group (Asteraceae: Gnaphalieae); (2) Axelius, 1990: Xanthophytum (Rubiaceae); (3) Boufford, et al., 1990: Circaea (Onagraceae); (4). Cox and Urbatsch, 1990: coneflower genera (Asteraceae: Heliantheae); (5) Cruden, 1991: Isidrogalvia (Liliaceae); (6) Gilmartin, et al., 1989: Glomeropitcairnia (Bromeliaceae); (7) Judd, 1989: Miconieae (Melastomataceae); (8) Kron and Judd, 1990: Rhodoreae (Ericaceae); (9) Lavin, 1990: Sphinctospermum (Leguminosae); (10) Loconte and Estes, 1989: Berberidaceae and Ranunculales

[2]The consistency index (CI) for a single character is m/s, where m is the minimum number of steps a character can show on any tree, and s is the minimum number of steps required on the tree under consideration. The ensemble CI for a suite of characters is M/S, where M and S are sums of m and s over all characters in the suite. The retention index (RI) for a single character is $(g-s)/(g-m)$, where m and s are as above, and g is the maximum number of steps that a character could require on any tree. The ensemble RI is analogous to the ensemble CI. For additional information see Farris (1989), Swofford (1990), and Maddison and Maddison (1992).