

METHODS AND TECHNIQUES

Patrocladistic classification

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Cladistic approaches to classification have become routine in plant systematics. Many workers now accept the following rules: (1) only synapomorphies are important for determining branching patterns (cladograms); (2) only holophyletic groups are acceptable; (3) classifications must be based directly upon these topological patterns; and (4) sister groups should have the same rank. Despite many positive aspects of cladistics, there remain several problems. Perhaps the most critical difficulty, and that which has led to the most discussion, is how to deal with character state evolution within lineages (i.e., the patristic divergence). This relates directly to the issue of recognition of paraphyletic groups. We present a new method for directly combining patristic and cladistic distances in an explicitly generated branching diagram (patrocladogram). This diagram can serve for classification using cladistic rules, because the patristic dimension has already been taken into account in the analysis. Controversial problems associated with paraphyletic groups vanish. Three examples are provided from plant groups at different levels of the taxonomic hierarchy with morphological and molecular data to suggest efficacy of the method.

KEYWORDS: apomorphies, cladistics, paraphyly, patristics, phylogeny

INTRODUCTION

For nearly a century from the time of Darwin's *Origin of Species* (1859) to the first phenetic paper by Michener & Sokal (1957), the theory of biological classification remained reasonably stable. Classifications were based on combinations of characters selected for presumptive evolutionary import. These phylogenetic (= phyletic or evolutionary) classifications took into consideration not only the branching pattern of phylogeny, but also divergence within lineages, all done without explicit methods (i.e., intuitively).

Biological classification has now changed dramatically within the past 50 years, the most notable changes being efforts to classify through explicit methods. The phenetic revolution (1957–1975; e.g., Sokal & Sneath, 1963) stressed concepts of characters and states, importance of the basic data matrix coded numerically, use of specific algorithms to determine affinity, and use of quantitative data to construct a branching diagram (phenogram). The cladistic revolution (1965–1990; e.g., Hennig 1966) emphasized using characters and states of high phylogenetic content, determination of polarity (= directionality) of these states, use of shared derived character states (synapomorphies) for determining relationships, and employment of new algorithms for building trees (cladograms).

Throughout its history, phenetics has remained eclectic, i.e., there have been numerous opinions and studies on how many characters to use, to weight or not to weight, and use of different algorithms for assessing relationships

as well as for constructing diagrams, not only in dendrogram form (phenogram) but also through coordinate plots (ordinations) in two- or three-dimensional space. No rigid rules for classification directly from these diagrams were ever adopted seriously.

Cladistics, in contrast, has gone through considerable theoretical and methodological change during its period of growth from 1965–1990. In the 1970s and 1980s occurred healthy efforts to seek different methods for tree construction, e.g., parsimony and character compatibility (e.g., Farris, 1970; Estabrook & al., 1976), but these began to narrow during the late 1980s nearly exclusively on parsimony. Due to the explosion of DNA studies and need for fast algorithms to deal with the mountains of new data, however, earlier phenetic algorithms have been recycled and are now being used routinely for tree construction (e.g., neighbor-joining). The utility of networks is also being examined carefully (Huson & Bryant 2006). Furthermore, interest has returned to reexamine the utility of compatibility methods (e.g., Pisani 2004). Algorithms based on models of evolution, such as maximum likelihood and Bayesian analysis, are now also routine for phylogeny reconstruction, especially with molecular data (Felsenstein, 2004).

Despite this new conceptual flexibility (or practicality) in cladistic analysis, the concepts of how to classify directly from a cladogram have not matured correspondingly. This has led to an acceptance by many workers of a series of rules, most important of which being that all groups must be holophyletic (i.e., those containing all descendants from a common ancestor; Ashlock, 1971; called

monophyletic by most workers). Paraphyletic groups, i.e., those that come from a common ancestor but do not contain all descendents (i.e., traditional definition of monophyly), are regarded as unacceptable.

The issue of whether or not to accept paraphyletic groups remains a central problem of biological classification (Nordal & Stedje, 2005; Williams & al., 2005; Hörandl, 2006). Although there are many evolutionary aspects to consider (Hörandl, 2007), the crux of the problem lies with character divergence within lineages, which strict cladistic classification does not take into account. We propose here a method of incorporating patristic distances, or evolutionary divergence within lineages, into an explicit method of producing a branching diagram (called a patrocladistic tree or patrocladogram). This dendrogram, because it already contains a measure of the patristic relationships among the taxa under study, can be used directly in classification by applying strict cladistic rules (especially the holophyletic criterion). We view this as most suitable for employment in groups that have obviously divergent members as revealed by tree construction (also often with conspicuous obvious morphological divergence). This should eliminate, or at least significantly reduce, the controversy over how to deal with paraphyletic groups. Discussion will rather shift to the characters and states involved with patristic distance and their relative weighting against synapomorphic character states. Such discussions on which characters and weights provide the best classifications are certainly not new in biological systematics and will doubtless never be resolved completely.

MATERIALS AND METHODS

The basis for patrocladistic classification is to first complete a cladistic analysis via any specific algorithm (parsimony, compatibility, Bayesian probability, maximum likelihood). Essential is to generate one selected tree, based on whatever support criteria, upon which to optimize the characters and states from the original data matrix. The distribution of apomorphies on the cladogram would usually be derived from the same analysis, but it would not have to be the case (apomorphies could be optimized on a neighbor-joining tree, for example). This is an important step, obviously, because different trees have different numbers of apomorphies that support the branches. The worker must decide which tree-building algorithm is more appropriate in the context of the particular group under investigation. Some trees will result in more homoplasious apomorphies than others, and this will obviously impact calculation of the patristic distances. Support levels should obviously also be high, as well as complete taxon sampling, as is the case with any attempt to derive a classification from a branching tree. This cladogram then serves as a

structure for modification based on patristic distance. Cladistic distances are calculated from the selected cladogram, and these are defined as the number of nodes that separate two taxa. These values are placed in a new cladistic matrix and are the basis for modification by addition of patristic distances. The patristic distance is defined as the number of apomorphic step changes separating two taxa on the cladogram. Unless only single synapomorphies define nodes in the cladistic analysis, the patristic distance will normally be larger than the cladistic distance. The patristic distance is then added to the cladistic distance to form the combined patrocladistic data matrix. These combined distances are used as input into a tree-building algorithm (or other phenetic methods such as UPGMA, single-linkage, etc.) for derivation of a modified branching pattern (the patrocladogram). We have used single-linkage in this paper because it more quickly connects groups and also more distinctly reveals dendrogram structure. Obviously, the greater the patristic distance within lineages, the more topological impact it will have on the patrocladogram. This new diagram, then, can be used in an explicit cladistic holophyletic (monophyletic) evaluation for classification.

Because the patristic distances will usually be larger than those from the cladistic pattern, they can be scaled and/or weighted (or deweighted) accordingly. For purposes of illustration, we have here transformed both cladistic and patristic distances to a scale between 0 and 1. Depending upon the evolutionary convictions of the particular worker, these values can also then be uniformly adjusted for their impact on the resultant topology. If the patristic distances were maintained and the cladistic distances reduced to nearly zero, the resulting diagram would approximate a phenogram, except that the characters were initially selected for their phylogenetic import (which is not usually the case with phenetics). How to weight the patristic vs. cladistic distances correctly in a theoretical context is not yet known. This must be assessed through tests of information content (and theory), which have rarely been applied to units of classification except in a strict cladistic context (e.g., Farris, 1979; see, however, also early broader steps in this direction by Duncan & Estabrook, 1976, and Carpenter, 1993).

To demonstrate the efficacy of the method, three examples are presented, two using morphological and one employing DNA sequence data. The first deals with the genera *Ammobium* and *Nabloomium* of Asteraceae (tribe Inuleae), which have been classified by Anderberg (1990, 1992). This represents a case of extreme divergence within a single lineage. The second deals with the traditionally recognized temperate families, Hippocastanaceae and Aceraceae, and their relationships to the tropical Sapindaceae based on morphological data (Judd & al., 1994). The third and final case is placement of the family Lactoridaceae relative to Aristolochiaceae and Piperales based on DNA sequence data (Qiu & al., 1999). Other molecular

datasets exist regarding relationships of Lactoridaceae (e.g., Qiu & al., 2005), but this is not pertinent in terms of presenting the method here. The three examples were chosen to demonstrate the utility of directly incorporating patristic evolutionary distance into a dendrogram that then forms the basis for classification, and to do so by use of both morphological as well as molecular data. The cladistic and patristic distances derived from these original papers are presented in Tables 1–3.

RESULTS

In the case of the *Ammobium-Nablonium* example (Figs. 1–2), it is obvious that incorporation of the patristic distance will have a large effect on the resultant den-

drogram. There is, in fact, more evolutionary character divergence (apomorphy) in the terminal lineage leading to *Nablonium* than within the rest of the entire cladogram (Fig. 1). Not surprisingly, with addition of patristic distance, the explicitly derived dendrogram changes (Fig. 2), whereby now the genus *Nablonium* is again supported by the patrocladistic topology. Both genera are now holophyletic. Orchard (1992) specifically argued for this viewpoint. For those workers wishing to incorporate divergence within lineages in their classifications, this simple example shows how it can be done quantitatively.

Hippocastanaceae and Aceraceae, both relatives of larger Sapindaceae, represent a more complex example based on morphological data. As is well known, the former two temperate families have long been recognized (e.g., Cronquist, 1981; Takhtajan, 1997). Judd & al. (1994), based on cladistic analyses of morphological features, presented a cladogram (Fig. 3) that shows clearly the distribution of the two families relative to the more inclusive and tropical Sapindaceae. Because recognition of Hippocastanaceae and Aceraceae as families would render Sapindaceae paraphyletic, all have been placed in Sapindaceae (see also Judd & al., 2002). As can be seen from the cladogram, however, numerous morphological synapomorphies define each of the two smaller families. A patrocladistic analysis of the morphological data reveals (Fig. 4) that with unweighted

Table 1. Matrix of cladistic (lower left) and patristic (upper right) distances among taxa of *Ammobium* and *Nablonium*.

	<i>A. alatum</i>	<i>A. craspedioides</i>	<i>N. calyceroides</i>
<i>A. alatum</i>		5	24
<i>A. craspedioides</i>	2		19
<i>N. calyceroides</i>	2	1	

Based on original data in Anderberg (1990).

Table 2. Matrix of cladistic (lower left) and patristic (upper right) distances among genera of Sapindales.

Genera	Genera																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Hypelate</i> (1)		18	18	18	13	14	8	8	13	10	13	17	17	20	21	23	23	29	29
<i>Aesculus</i> (2)	5		2	4	19	20	14	20	25	22	25	29	29	32	33	35	35	41	41
<i>Billia</i> (3)	5	1		4	19	20	14	20	25	22	25	29	29	32	33	35	35	41	41
<i>Handeliodendron</i> (4)	4	2	2		19	20	14	20	25	22	25	29	29	32	33	35	35	41	41
<i>Delevaya</i> (5)	5	5	5	4		7	5	15	20	17	20	24	24	27	28	30	30	36	36
<i>Ungnadia</i> (6)	5	5	5	4	1		6	16	21	18	21	25	25	28	29	31	31	37	37
<i>Koelreuteria</i> (7)	4	4	4	3	2	2		10	15	12	15	19	19	22	23	25	25	31	31
<i>Talisia</i> (8)	3	5	5	4	5	5	4		7	4	7	11	11	14	15	17	17	23	23
<i>Euphoria</i> (9)	4	6	6	5	6	6	5	2		5	8	12	12	15	16	18	18	24	24
<i>Sapindus</i> (10)	5	7	7	6	7	7	6	3	2		3	7	7	10	11	13	13	19	19
<i>Cupania</i> (11)	6	8	8	7	8	8	7	4	3	2		6	6	9	10	12	12	18	18
<i>Thinonia</i> (12)	7	9	9	8	9	9	8	5	4	3	2		4	7	8	10	10	16	16
<i>Thouinia</i> (13)	8	10	10	9	10	10	9	6	5	4	3	2		5	6	8	8	14	14
<i>Athayana</i> (14)	9	11	11	10	11	11	10	7	6	5	4	3	2		5	7	7	13	13
<i>Serjania</i> (15)	10	12	12	11	12	12	11	8	7	6	5	4	3	2		6	6	12	12
<i>Bridgesia</i> (16)	11	13	13	12	13	13	12	9	8	7	6	5	4	3	2		4	10	10
<i>Diatenopteryx</i> (17)	12	14	14	13	14	14	13	10	9	8	7	6	5	4	3	2		8	8
<i>Dipteronia</i> (18)	13	15	15	14	15	15	14	11	10	9	8	7	6	5	4	3	2		2
<i>Acer</i> (19)	13	15	15	14	15	15	14	11	10	9	8	7	6	5	4	3	2	1	

Based on original data in Judd & al. (1994); order of genera following their cladogram.

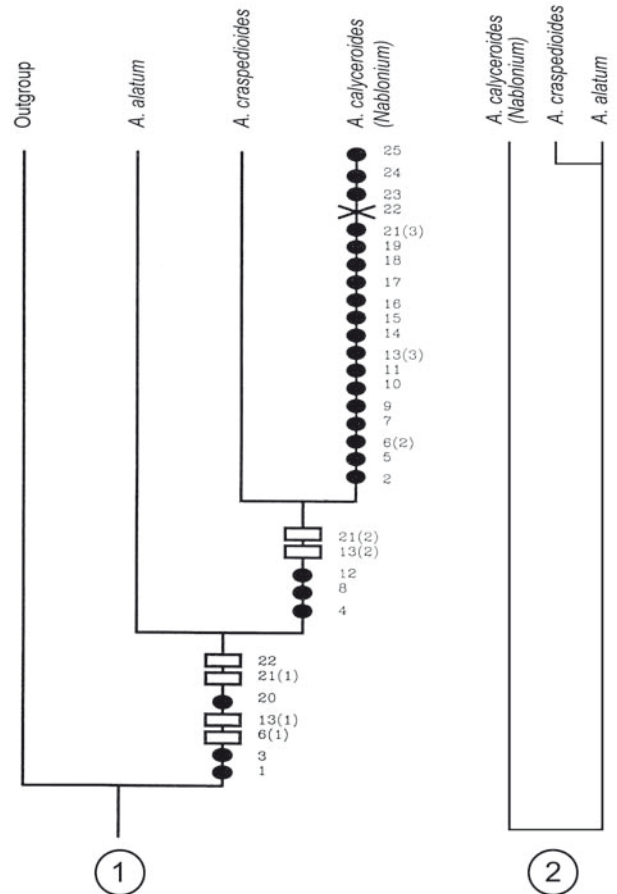
Table 3. Matrix of cladistic (lower left) and patristic (upper right) distances among genera of Piperales and Winterales.

Genera	Genera															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Anemopsis</i> (1)		122	141	429	287	439	445	469	358	344	417	390	387	388	427	425
<i>Saururus</i> (2)	1		155	443	301	453	459	483	372	358	431	404	401	402	441	439
<i>Houttuynia</i> (3)	2	2		426	284	436	442	466	355	341	414	387	384	385	424	422
<i>Peperomia</i> (4)	4	4	3		244	642	648	672	561	547	620	593	590	591	630	628
<i>Piper</i> (5)	4	4	3	1		500	506	530	419	405	478	451	448	449	488	486
<i>Aristolochia</i> (6)	7	7	6	6	6		68	336	293	279	412	385	382	383	422	420
<i>Thottea</i> (7)	7	7	6	6	6	1		342	299	285	418	391	388	389	428	426
<i>Lactoris</i> (8)	6	6	5	5	5	2	2		323	309	442	415	412	413	452	450
<i>Asarum</i> (9)	6	6	5	5	5	4	4	3		66	331	304	301	302	341	339
<i>Saruma</i> (10)	6	6	5	5	5	4	4	3	1		317	290	287	288	327	325
<i>Bellium</i> (11)	9	9	8	8	8	9	9	8	8	8		51	54	69	228	226
<i>Drimys</i> (12)	9	9	8	8	8	9	9	8	8	8	1		27	42	201	199
<i>Tasmannia</i> (13)	8	8	7	7	7	8	8	7	7	7	2	2		39	198	196
<i>Takhtajania</i> (14)	7	7	6	6	6	7	7	6	6	6	3	3	2		199	197
<i>Canela</i> (15)	7	7	6	6	6	7	7	6	6	6	5	5	4	3		40
<i>Cinnamodendron</i> (16)	7	7	6	6	6	7	7	6	6	6	5	5	4	3	1	

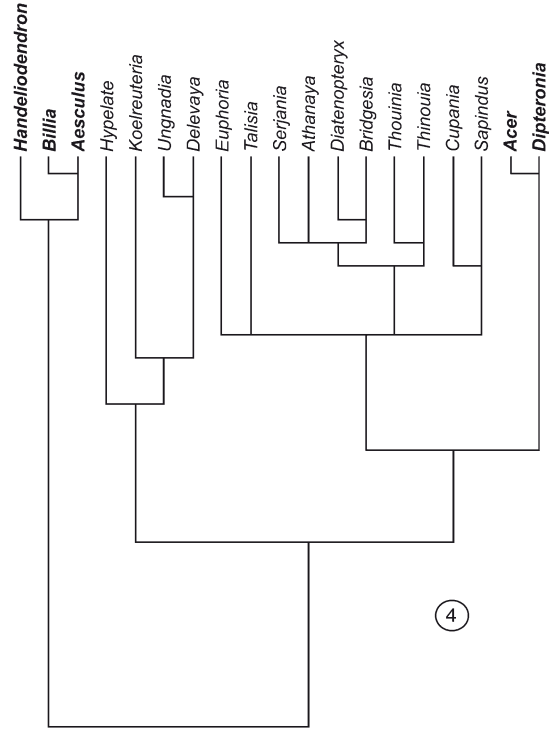
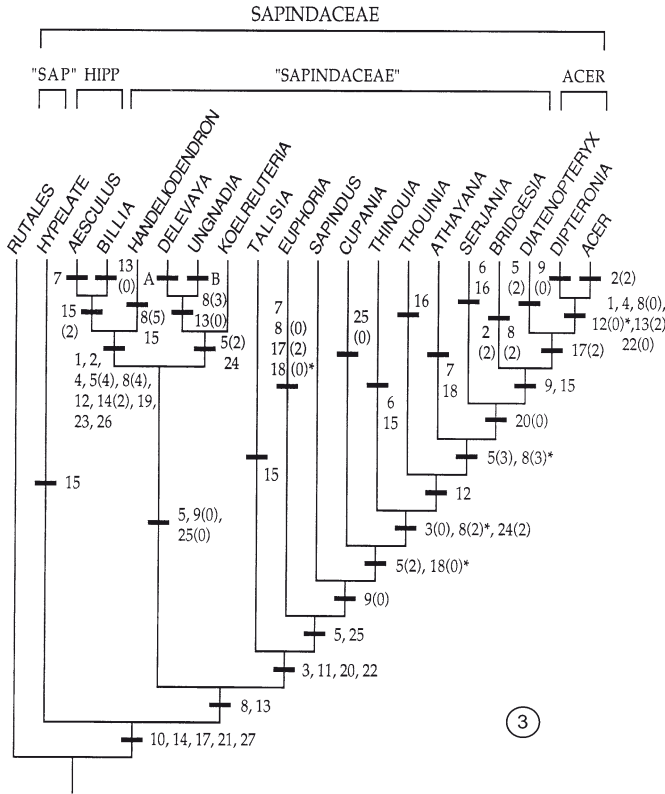
Based on original data in Qiu & al. (1999); order of genera following their cladogram.

patristic data, both groups separate considerably, with Hippocastanaceae (including *Handeliidendron*) becoming the sister group of all the rest. Aceraceae, however, remain embedded within Sapindales, a position favored by Chase & al. (2000). It is also worth mentioning that based on molecular data the recognition of these two temperate families remains unresolved (Gadek & al., 1996).

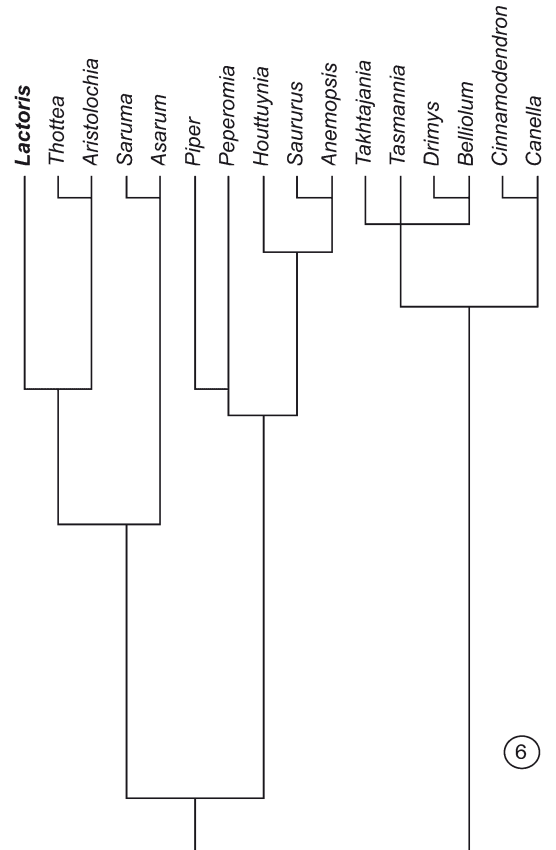
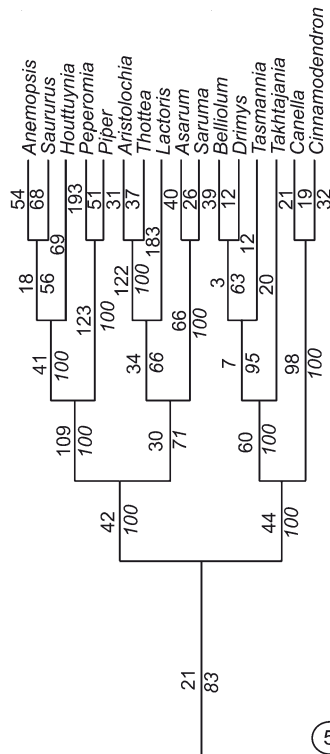
The final example concerns the very interesting ancient family Lactoridaceae (for a review of features see Stuessy & al., 1998). This is a monospecific family (with *L. fernandeziana*) confined today to the Juan Fernandez (Robinson Crusoe) islands in the eastern Pacific Ocean off the coast of Chile. Although presently restricted to Masatierra Island, known radiometrically at c. 4 million years of age (Stuessy & al., 1984), fossil pollen has been found in deep sea sediments off the western coast of Africa (Zavada & Benson, 1987) and northern coast (and on the continent) of Australia (Macphail & al., 1999) at 70–90 my and 50–80 my, respectively. It has long been regarded as one of the ancient angiosperm families (e.g., Meeuse, 1971). As with many ancient taxa with unusual morphological combinations, however, Lactoridaceae have been difficult to relate to



Figs. 1–2. Dendrograms of relationships of species of *Ammobium* and *Nablonium* (Asteraceae) based on morphological data. Fig. 1. Cladogram from Anderberg (1990); dots = apomorphies (CI = 1), rectangles = apomorphies (CI < 1), X = reversal. Fig. 2. Corresponding patrocladogram, single linkage, with cladistic and patristic distances transformed and equally weighted.



Figs. 3–4. Dendrograms of relationships among genera of Sapindaceae (s.str.), Aceraceae and Hippocastanaceae (Sapindales) based on morphological data. Fig. 3. Cladogram from Judd & al. (1994); * = one or more alternative placements are equally parsimonious; A and B refer to three and four character state changes, respectively. Fig. 4. Corresponding patrocladogram, single linkage, with cladistic and patristic distances transformed and equally weighted.



Figs. 5–6. Dendrograms of relationships among genera of basal angiosperms based on five-gene DNA sequence data. Fig. 5. Cladogram from Qiu & al. (1999); numbers are branch lengths, those in italics bootstrap percentages. Fig. 6. Corresponding patrocladogram, single linkage, with cladistic and patristic distances transformed and equally weighted.

other families (e.g., Lammers & al., 1986), with Magnoliales and Laurales being the more frequent previous placements. Recent anatomical and molecular studies, however, have pointed clearly to a position in Piperales (Carlquist, 1990; González & Rudall, 2001). Some DNA data, at least, have gone further and suggested placement within Aristolochiales (Fig. 5). Results of patrocladistic classification based on molecular data reveal that Lactoridaceae remain embedded within Aristolochiaceae. Based on these molecular data and patrocladistic analyses, therefore, the reasonable view is that Lactoridaceae belong best in Aristolochiaceae. With other data, such as morphology or even other molecular sequences, however, the results might be different.

DISCUSSION

The emphasis on quantitative methods of classification that developed from phenetic and cladistic innovations during the past 40 years can only be viewed as positive. Methods that require clarity of data employed and explicit algorithms for assessing relationships have greatly accelerated our understanding of classification and reconstruction of phylogeny. Whatever one's view of success or failure of specific approaches, these past decades have resulted in much disciplinary progress.

The success of cladistic analysis, in part fueled by need to deal with the mountains of new DNA sequence data, has resulted in a set of "rules" that are adhered to by many practitioners: (1) only synapomorphies are important for determining branching patterns (cladograms); (2) only holophyletic (monophyletic) groups are acceptable; (3) classification must be based directly upon these topological patterns; and (4) sister groups should have the same rank. The fourth point has not been emphasized as much as the others, and significant differences of opinion (or preference) still exist.

The most controversial point has been the acceptance of only holophyletic (monophyletic) groups in classification, i.e., that a taxon must include its ancestor and all descendents. In other words, this is rejection of paraphyly, in which taxa include ancestors and descendents, but *not all* descendents. That this issue is still controversial is attested to by the recent points of view of Nordal & Stedje (2005), Williams & al. (2005), and Hörandl (2006), among numerous others. The issue of whether to formally recognize paraphyletic groups in classification relates directly to patristic distance within a phylogeny. Divergent single taxa may be very different in character composition from its closest relatives, even though it must tie, based on the bifurcating topology of the trees, to some sister group in the cladogram. Recognizing the highly divergent taxa formally, which renders the remaining taxa paraphyletic, has been the crux of the issue (such as the *Ammobium–Nablonium* example). In

our opinion, because autapomorphies that define a taxon as widely divergent have been selected originally for their presumptive evolutionary content at the start of the cladistic analysis, they have already been judged important for classification. To ignore them, therefore, is to discard data, being hardly objective, and falls clearly outside acceptable explicit approaches to classification. The question is how to deal with this effectively. Several other suggestions have been offered (e.g., Estabrook, 1986; Stuessy, 1987, 1997; Hall, 1988; Ashlock, 1991), but none of them has caught the attention of workers for routine classification, perhaps due to lack of user-friendly computer programs for their implementation (Hörandl, 2006).

For any method of biological classification, desirable is to have guidelines for formal recognition of groups. Cladistics does this first by accepting the topology of the cladogram and, especially with molecular data, calculating support values for each node. Common measures of support are the bootstrap, jackknife, and Bremer (decay) values. Based on this information, and in applying the concept of holophyly, taxa are formed. Informal and formal ranking often follow immediately thereafter, with sister taxa accorded the same rank. It is important to emphasize that there is no absolute level of branch support that requires taxon recognition. The higher the bootstrap, for example, the more confidence we place in the tree, and hence the resultant classification. Values above 80% inspire confidence and values below less so, but this is only a guideline.

Patrocladistics also offers estimates of support for taxon recognition. First, the initially selected cladogram from which we calculate the cladistic and patristic distances should be well supported. Second, we can examine the apomorphic support and apomorphic difference of the taxon in question following suggestions of Stuessy (1997). For apomorphic support (as %), this involves dividing the number of apomorphic character state changes leading to the group by the total number of step changes in the cladogram. For apomorphic difference of each taxon (or clade), we take the average of the difference in apomorphic support between it and all pairs of taxa (and clades). These two values are plotted in a graph such that taxa that are highly divergent with both means of support are clearly seen and can be recommended for recognition (Figs. 7–9). In Fig. 7, it is obvious that *A. calyceroides* is very highly supported by apomorphies and distinct from the other two taxa. This argues strongly for generic recognition. In Fig. 8, *Aesculus* with *Bililia* and *Handeliendron* are highly supported apomorphically and also relatively divergent from the other groups. This argues for familial status for Hippocastanaceae (including *Handeliendron*). Support for Aceraceae (*Acer* and *Dipteronia*) is less strong. In Fig. 9, there is no strong apomorphic support for *Lactoris* as a separate family in isolation, but it is nonetheless divergent (as is also *Peperomia*).

Another means of support can be derived from the

patrocladistic analysis. If addition of simple unweighted (or only fractionally weighted, $\times 0.1$ – 0.9) patristic distance results in two holophyletic taxa, then this by itself is a very strong argument for their recognition as sister groups. If with unweighted patristic distance the groups do not separate holophyletically, then the question focuses on how much the patristic distance must be weighted ($\times 1.1$, 1.2 , 1.3 , etc.) so that the taxa do separate. We suggest that between $\times 0.1$ and 0.9 is the region of clearly acceptable support in a patrocladistic context (Fig. 10), $\times 1.0$ – 1.9 being still worthy of consideration, but $\times 2.0$ and above being simply too extreme an emphasis on patristic distance. One can elect to emphasize any level of patristic support based on the particular characters and states involved, obviously, just as one can also do with nodal support values in a cladistic context. At the very least, the reasons for such a decision can be made explicit and the results communicated clearly. Figure 10 also shows the results of this analysis with the three groups used as examples in this paper. The distinctness of *Nablonium* is obvious, and it should be recognized as a separate genus. With respect to Hippocastanaceae, with *Handeliodendron* included this family also is strongly supported for recognition. For *Acer* and *Dipteronia* to become holophyletic relative to the rest of Sapindaceae, the patristic distance must be weighted more than $\times 2$, which would be difficult to justify in our opinion. *Lactoris* does not resolve holophyletically even after $\times 4$ patristic weighting.

The method recommended here, patrocladistic classification, admits importance of patristic distance in classification and provides a simple method of incorporating these data in a reconstructed branching diagram (patrocladogram), which then can be judged by cladistic rules. We are well aware that not all workers will be satisfied with this method for various reasons, least of all because it is not strictly cladistic. Nonetheless, we see no reason why

classification must be constrained by a branching topology solely in a cladistic context. What needs to be done in biological classification is to further address information content of classifications. Information can be defined in many ways. Cladistics has defined it in context of minimum data required for support of a branching topology. But there are other measures, such as involving predictive quality of data contained within a matrix, as shown by Duncan and Estabrook (1976) and Carpenter (1993). It may be impossible for systematic biologists to agree on a suitable definition of information content in classification, but at very least, studies should be directed at this problem to understand better the options.

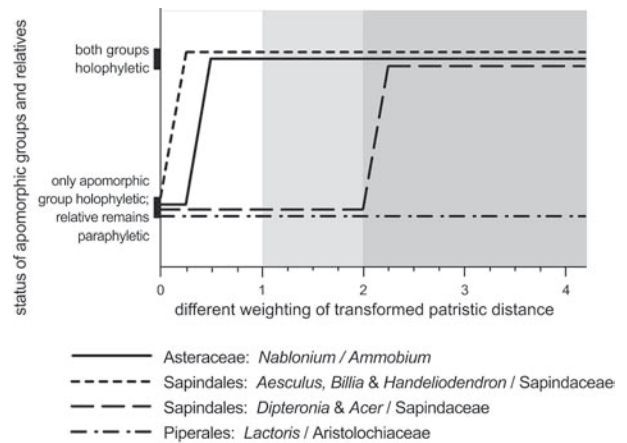
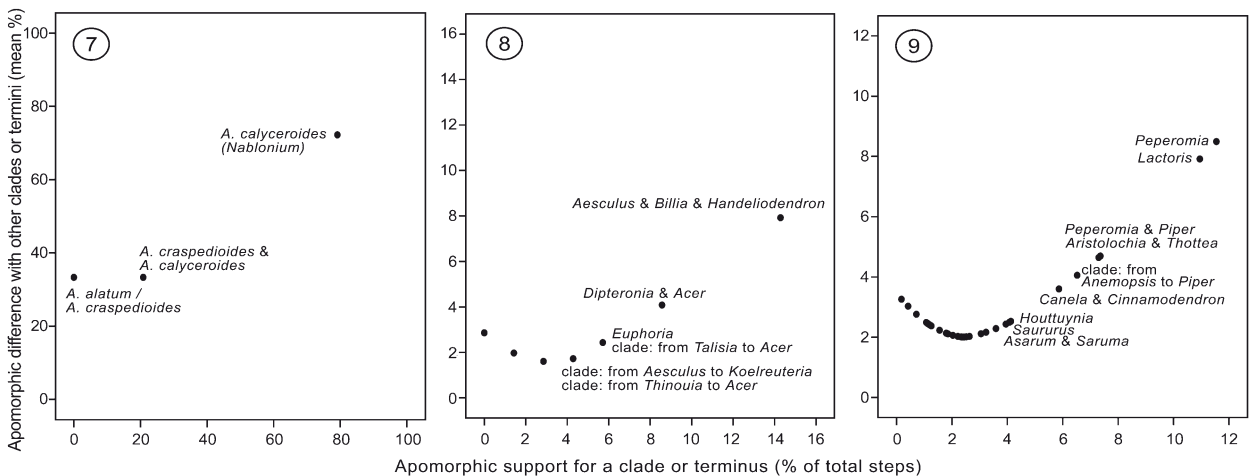


Fig. 10. Plotting of results from patrocladistic analyses showing topological change in patrocladogram (toward holophyly in both apomorphic group and relatives) based on increasing levels ($\times 0$ – 4.0) of transformed patristic weighting. Degrees of shading suggest levels of taxonomic acceptance of groups (0– 0.9 , acceptable; 1.0 – 1.9 , less acceptable; ≥ 2 , unacceptable)



Figs. 7–9. Plotting of apomorphic support versus apomorphic divergence for species of *Ammobium* and *Nablonium* (Fig. 7), genera of Sapindaceae s.l. (Fig. 8), and genera of Piperales and Winterales (Fig. 9), based on original cladograms (Figs. 1, 3, 5). See Tables 1–3 for full taxon names.

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