Progress and Prospects in Reconstructing Plant Phylogeny

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PROGRESS AND PROSPECTS IN RECONSTRUCTING PLANT PHYLOGENY[1]

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ABSTRACT

Phylogeny reconstruction has become respectable science over the last few decades, and trees are accumulating rapidly in the literature. Botanists have been active in this effort and can already cite success stories (e.g., recognition of streptophytes, stomatophytes, anthophytes, eudicots). Nevertheless, only a small number of problems have been addressed and some of these have resisted solution. To solve the toughest problems, especially those involving ancient, rapid radiations, various sources of data will need to be combined, including evidence from fossils. Furthermore, in view of limitations in analyzing data sets with many taxa, more attention must be paid to the consequences of different taxon sampling strategies and to how large, variable taxa can be represented in more inclusive studies.

Over the next few years we should continue to move toward a phylogenetic system (monophyletic groups defined by ancestry, diagnosed by characters), which will entail the elimination of familiar paraphyletic taxa. We can expect increased use of phylogenies by ecologists, molecular biologists, and others, which will force us to attend to the issue of the reliability of phylogenetic hypotheses, and will necessitate the development of a database of phylogenetic studies. Interactions with population biologists promise to be especially productive, since there are obvious mutual concerns centered on the analysis of gene trees and reticulation.

Over twenty-five years have elapsed since the publication of Willi Hennig's *Phylogenetic Systematics* (Hennig, 1966), and for well over a decade botanical systematists have been conducting numerical phylogenetic analyses. The focus of the Missouri Botanical Garden's Annual Systematics Symposium on the "Origin and Relationships of the Major Plant Groups" suggests that progress has been made, and the meeting itself documented significant advances in our understanding of several of the most challenging phylogenetic questions. The aim of this paper is to take stock, in general terms, of where things stand. Has phylogenetic analysis had a substantial impact on our understanding of plant phylogeny, and where do we go from here?

PROGRESS

Although many of the ideas underlying phylogenetic analysis have a rather long history (see Craw, 1992; Donoghue & Kadereit, 1992), phylogeny reconstruction has become respectable science only over the last few decades. This happy circumstance can be traced to a series of developments in the logic of phylogeny reconstruction (e.g., Hennig, 1966; Farris, 1983; see Sober, 1988; Swofford & Olsen, 1990), to the availability of computers and algorithms to implement this logic (e.g., Farris, 1988; Maddison & Maddison, 1992; Swofford, 1993), and to new sources of evidence, especially molecular data (e.g., Fernholm et al., 1989; Hillis & Moritz, 1990). While it is obvious that these developments have had a significant impact on plant systematics, it is not entirely clear how best to measure the progress that has been made. There are, however, several indicators that bear consideration.

LEVEL OF ACTIVITY

One measure of progress is simply the rate of publication of phylogenetic hypotheses. Phylogenetic trees are undoubtedly accumulating in the literature, but the magnitude of the effort is difficult to assess because no one has been keeping track of such information. In a survey of 79 journals published in 1989, 1990, and 1991, we recently assembled data on 1140 articles that contained trees (Sanderson et al., 1993). This remarkable number of studies (nearly a tree a day) is surely

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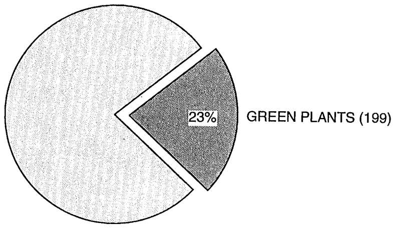
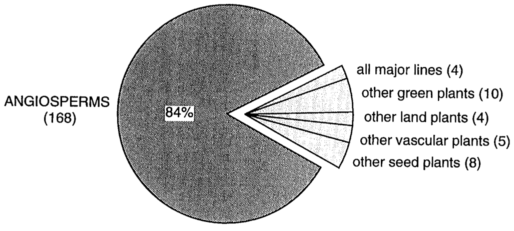
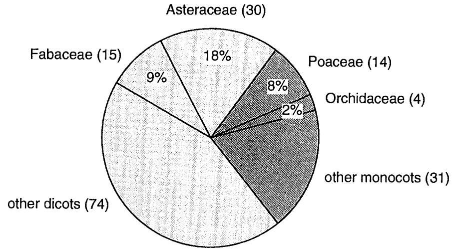


882 PHYLOGENETIC STUDIES (1989-91)



199 GREEN PLANT STUDIES (1989-91)



168 ANGIOSPERM STUDIES (1989-91)

FIGURE 1. Pie charts showing aspects of the taxonomic distribution of numerical phylogenetic studies published between 1989 and 1991 (compiled from an updated version of a database assembled by Sanderson et al., 1993). Top: Studies of green plants (chlorophytes; with chlorophyll b, starch storage) account for ca. 23% of the 882 phylogenetic analyses in the Sanderson et al. database. Middle: Approximately 84% of the green plant studies are of angiosperm groups; the remainder are of "other seed plants" (specifically conifers, cycads), "other vascular plants" (ferns, lycopsids), "other embryophytes" (mosses, liverworts), "other green plants" (various "green algae"), or included representatives of "all major lines." Bottom: Of 168 angiosperm studies, 49 (ca. 29%) are of monocot groups; Asteraceae and Fabaceae account for ca. 38% of the "dicot" studies.

an underestimate inasmuch as we did not survey every journal containing phylogenetic studies and we were unable to include analyses published in books. Nevertheless, our study probably provides a reasonably accurate picture of what exists in the literature. Of the total, 882 (77%) of the studies employed some "cladistic" method (including parsimony and some distance methods, but not phenetic clustering methods such as UPGMA), and over 471 (53%) of the phylogenetic studies used some form of molecular evidence (including allozyme data), with the percentage of such studies increasing from 51% to 56% over the three-year period.

We identified 312 studies of green plant groups (ca. 27% of the total), namely organisms with chlorophyll b and starch storage, including the various lines of "green algae" and the land plants (Sanderson et al., 1993). However, 113 (36%) of these employed only phenetic techniques, a greater percentage of phenetic studies than we found in any other major group of eukaryotes. A breakdown of the remaining 199 numerical phylogenetic studies of green plants (ca. 23% of all phylogenetic studies) is shown in Figure 1. The vast majority (168, 84%) of these were of angiosperm groups. Within angiosperms, Asteraceae (30 phylogenetic studies) and Fabaceae (15 studies) received the most attention, while other large families, such as Orchidaceae (4 studies) are underrepresented. The 49 studies of monocots account for around 29% of all angiosperm studies, with 14 of these within grasses. To some extent these numbers reflect the number of species per group, but historical factors are evident as well. For example, studies of Asteraceae were stimulated by the early and promising restriction site studies of Jansen, Palmer, and colleagues (see references in Palmer et al., 1988; Jansen et al., 1992).

Figure 1 also shows that some groups have received relatively little attention, especially considering their importance in understanding phylogenetic relationships among major lines of green plants. For example, we found only five phylogenetic analyses of vascular plants other than seed plants during the three-year period, despite their great phylogenetic significance and the evident interest of pteridologists in phylogenetic questions (e.g., Wagner, 1980). Such studies, including fossil groups (e.g., "Cladoxylales," "Coenopteridales," and "progymnosperms"), are desperately needed in order to establish, for example, whether eusporangiate fern groups are more closely related to leptosporangiate ferns or perhaps to progymnosperm groups (and hence seed plants). Fortunately, zosterophylls and lycophytes (including fossils) are now receiving more attention (e.g., Bateman et al., 1992; Gensel, 1992).

Although the absolute number of molecular studies of green plant phylogeny increased slightly each year, the percentage of such studies over the three-year period fluctuated around 50%, the rest being based on morphology and/or secondary chemistry. Overall, about half of the molecular studies were based on restriction fragment variation, especially in chloroplast DNA. The number of plant studies based on nucleotide sequences has risen dramatically since 1991 (e.g., studies of the chloroplast gene *rbc*L), and will undoubtedly continue to increase in number, but rather few such studies (32, 24% of the plant molecular studies) were published in the 1989–1991 period. Over half of the sequence studies involved ribosomal genes (see Zimmer et al., 1989; Hamby & Zimmer, 1992; Waters et al., 1992), and in the near future, especially at lower taxonomic levels, analyses of the internal transcribed spacer (ITS) regions (e.g., Baldwin, 1992; Wojciechowski et al., 1993) promise to be productive. Phylogenetic studies using "single-copy" nuclear genes are still rare, but technical difficulties in obtaining such sequences have been largely overcome, and I expect that they will play an increasingly important role.

Phylogenetic studies that include fossils are still rare, despite their potential significance (Donoghue et al., 1989).While molecular studies of fossils are promising (e.g., Golenberg et al., 1990; Soltis et al., 1992), their impact will depend on developing the ability to repeatably obtain significant segments of DNA from plant parts fossilized in standard ways.

SUCCESS STORIES

While it is obvious that botanists have actively engaged in phylogenetic research, it is more difficult to determine how successful these efforts have been. However, in several cases significant progress does appear to have been made. Some of these successes are highlighted in the accompanying symposium papers, so only a few are noted here (Fig. 2).

The studies by Mishler and colleagues (see Mishler et al., 1994, this issue) have confirmed earlier indications that green algal groups with phragmoplasts, especially charophytes such as *Coleochaete*, are more closely related to land plants than they are to other "green algae." They also solidify the view that "bryophytes" are paraphyletic, with mosses more closely related to tracheophytes. These hypotheses are being borne out by molecular evidence (Mishler et al., 1992, 1994).

Kenrick & Crane (1991) have made great progress in establishing relationships among early lines of vascular plants, suggesting that several major splitting events and morphological innovations predated the radiation giving rise to extant groups. Their detailed studies of tracheids, coupled with the remarkable discoveries of Remy and colleagues on gametophyte morphology (e.g., Remy, 1982; references in Kenrick & Crane, 1991), provide excellent examples of the importance of fossils in understanding the early evolution of vascular plants. Again, these conclusions are consistent with recent molecular evidence (e.g., Palmer et al., 1988; Manhart & Palmer, 1990; Raubeson & Jansen, 1992).

Morphological phylogenetic analyses of seed plants (Crane, 1985, 1988; Doyle & Donoghue, 1986, 1992; Loconte & Stevenson, 1990; Doyle et al., 1994, this issue; Nixon et al., 1994, this issue), while not agreeing in detail, have consistently concluded that Gnetales are the living group most closely related to angiosperms (Fig. 2). This clade is also supported (though not very strongly) by chloroplast and ribosomal sequence data (Chase et al., 1993; Hamby & Zimmer, 1992; but see Troitsky et al., 1991; Hasebe et al., 1992). An "anthophyte" clade, consisting of these two living groups plus Bennetittales and *Pentoxylon*, is a regular feature of the studies that have included fossils. Furthermore, with the exception of some analyses by Nixon et al. (1994), all of these studies have determined that Gnetales are monophyletic, with *Gnetum* and *Welwitschia* more closely related to one another than either is to *Ephedra*. In this case, the molecular data are especially compelling (Doyle et al., 1994).

There has also been consensus on the monophyly of angiosperms, a significant conclusion in view of lingering adherence to the belief that they are polyphyletic (e.g., Krassilov, 1991). Within angiosperms there have also been promising results. Perhaps most importantly, the "tricolpate" clade of Donoghue & Doyle (1989; "eudicots" of Doyle & Hotton, 1991) has surfaced in recent *rbc*L studies (Olmstead et al., 1992; Chase et al., 1993), implying that the vast majority of "dicots" (the "higher" subclasses of Cronquist, 1988; Takhtajan, 1987) form a clade, as opposed to having several separate origins among "magnoliids," as suggested previously. Further analyses are needed to check the robustness of this conclusion.

Even from this short list it is clear that "success" has not been tied to the use of any one type of evidence. In fact, the very impression of success stems from "making sense" of all of the data, including information on fossil and Recent organisms, morphology and molecules. In stressing this "criterion of veracity," Hennig (1966) provided a characteristically convincing analogy, which I have reproduced in Figure 3. In this example, the process of accounting for all of the evidence is likened to a geographer attempting to assemble the torn pieces of a map so as to bring together all of the

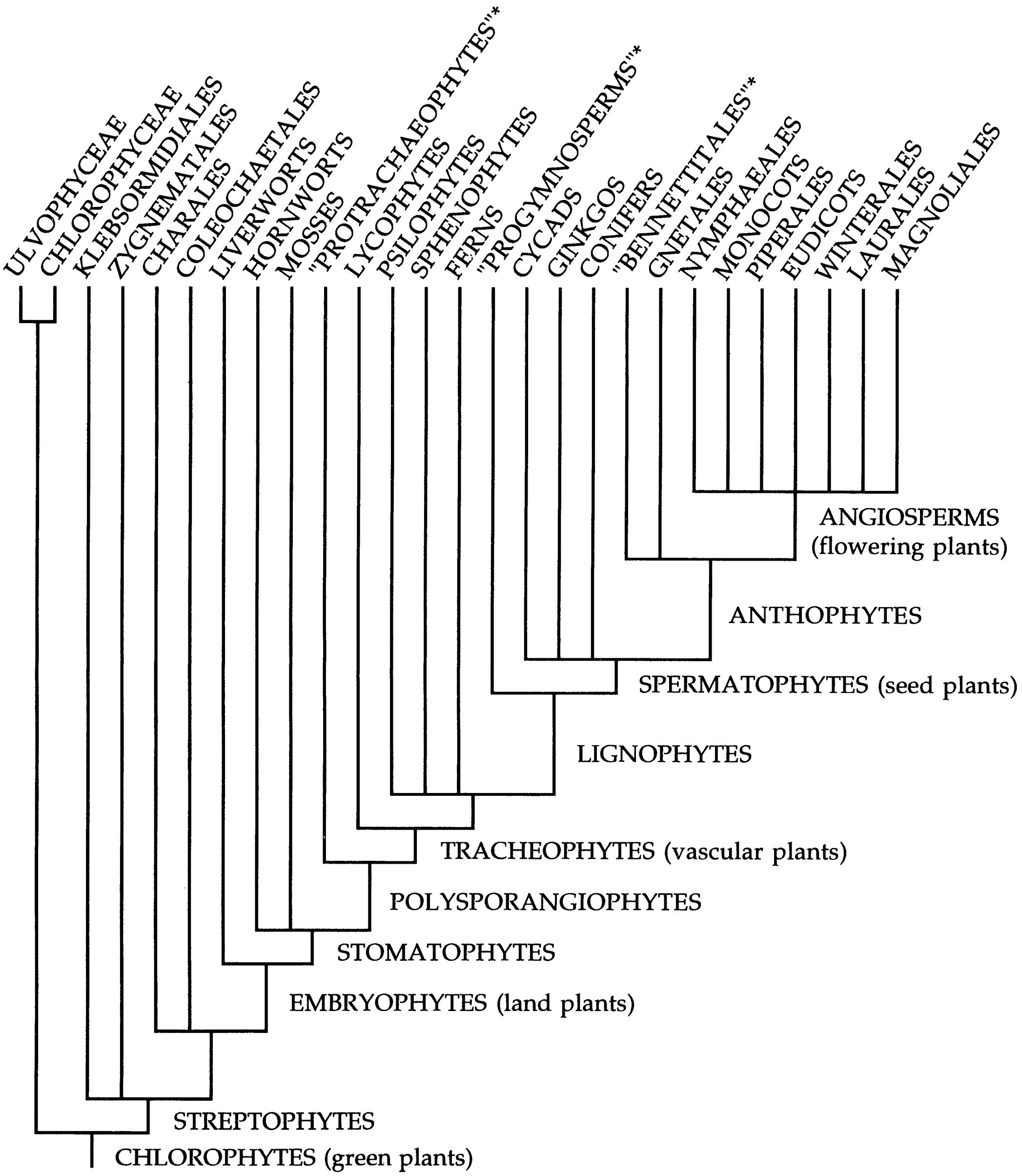


FIGURE 2. An overview of green plant phylogeny (based on analyses cited in the text), showing major clades that seem reasonably well supported and areas of continuing uncertainty (unresolved polychotomies). Many groups are omitted, and resolution is simplified to highlight familiar clades (see O'Hara, 1992). Only three fossil groups are included (marked by *), which are probably paraphyletic (quotation marks). Some of the best supported branches have long been recognized (e.g., land plants, seed plants, flowering plants), though these have not been universally accepted; others have been re-circumscribed (e.g., tracheophytes) or named (e.g., polysporangiophytes) only recently (Kenrick & Crane, 1991); several others have not yet been named (e.g., Charales+Choleochaetales+Embryophytes). Recognition of the monophyly of a number of terminal taxa (e.g., eudicots) is also an outcome of recent phylogenetic studies. Note that some traditional groups (e.g., "green algae," "bryophytes," "gymnosperms") are not monophyletic, and are not shown.

roads, rivers, and other landmarks. The corresponding operation in phylogenetic systematics is assessing, as Hennig (1966: 130) put it, "whether the differently determined views concerning the phylogenetic relationships of different groups of organisms are in agreement." Satisfaction is achieved when the pieces are assembled so that everything fits. One of the central points of the example is that a perfectly consistent explanation for any one road, or bit of evidence, might turn out to be highly unparsimonious when other features, however minor they may have seemed at the outset, are taken into consideration.

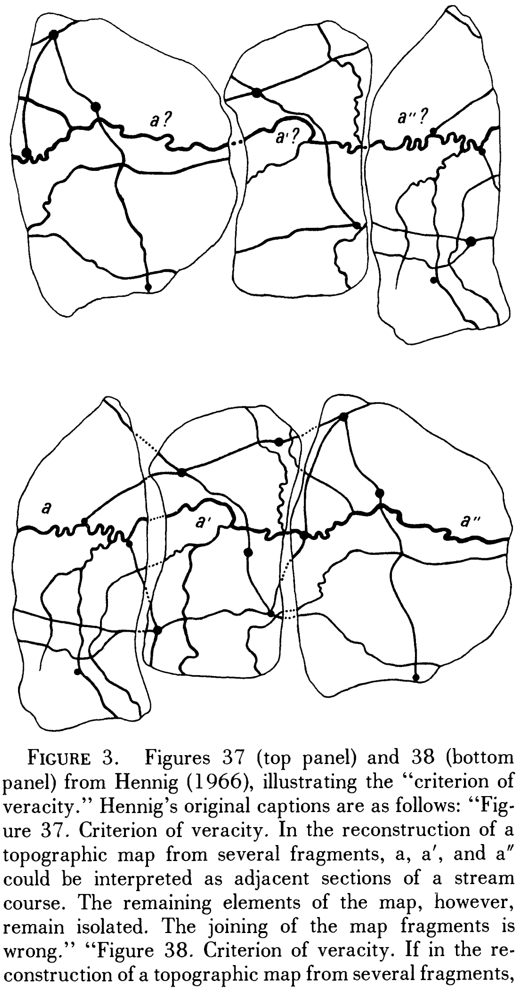


FIGURE 3. Figures 37 (top panel) and 38 (bottom panel) from Hennig (1966), illustrating the "criterion of veracity." Hennig's original captions are as follows: "Figure 37. Criterion of veracity. In the reconstruction of a topographic map from several fragments, a, a', and a″ could be interpreted as adjacent sections of a stream course. The remaining elements of the map, however, remain isolated. The joining of the map fragments is wrong." "Figure 38. Criterion of veracity. If in the reconstruction of a topographic map from several fragments, a, a', and a″ are interpreted as adjacent sections of a stream, the other elements of the map also join to form a sensible illustration. The joining of the map fragments is correct."

OUTSTANDING PHYLOGENETIC PROBLEMS

For each success story there are, of course, many other problems that have not been addressed or for which a satisfying result has not yet been obtained. Thus, as also shown in Figure 2, relationships among the major extant lines of seed plants (cycads, ginkgos, conifers, anthophytes) have not yet been convincingly resolved (Doyle & Donoghue, 1992; Doyle et al., 1994). Likewise, the position of the root of angiosperms, whether among "magnoliids" or among "paleoherbs," has remained unsettled (but see Doyle et al., 1994). In both cases, particular data sets fail to provide convincing support for one hypothesis over another and/or there are conflicts among the results based on different data sets. Even in these cases, however, some hypotheses appear less likely to be true than others. For example, there is little evidence that the root of angiosperms is among monocots, and I find it interesting that molecular data in particular do not support rooting the tree in the vicinity of Chloranthaceae. Furthermore, it is worth noting that conflicts appear to be as significant *among* different molecular trees (contrast Martin & Dowd, 1991; Hamby & Zimmer, 1992; Chase et al., 1993), and *among* different morphological results (contrast Dahlgren & Bremer, 1985; Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Taylor & Hickey, 1992; Nixon et al., 1994), as they are *between* molecular and morphological results.

What can be done to solve such problems? First, we can hope to obtain more decisive data. New molecular evidence will certainly be forthcoming, and traditional sources of evidence are far from being exhausted. Much of the information present in standard compendia (e.g., Cronquist, 1981) has not yet been incorporated in phylogenetic analyses. This can and should be done, but will require a critical reassessment of homology hypotheses (Donoghue & Sanderson, 1994). Furthermore, new approaches to morphology, such as detailed studies of flower development and function (e.g., Endress, 1987; Tucker, 1988; Erbar, 1991; Williams et al., 1993), continue to provide valuable phylogenetic characters. Comparative analyses that make use of recent findings on the molecular mechanisms underlying flower development (e.g., Coen & Meyerowitz, 1991) promise to be especially useful in elucidating the homology of the structures that have been most heavily used in morphological phylogenetic research.

Different sources of evidence also can be combined and analyzed simultaneously (Kluge, 1989; Barrett et al., 1991; Donoghue & Sanderson, 1992; but see Swofford, 1991; Bull et al., 1993; de Queiroz, 1993). Here the hope is that weak signals present in several separate data sets might complement one another and provide a single stronger result. Obviously, this need not be the outcome, but it behooves us to explore such possibilities in particular cases. In the case of the angiosperm root, the combined analysis of Doyle et al. (1994) favors a placement among paleoherbs more convincingly than any single data set. This is not simply a matter of a larger number of molecular characters swamping out the morphological evidence, because some elements in the combined trees are more consistent with morphology. The temptation to compete molecules against morphology is simply counterproductive—combining the evidence may provide the best hope of success (Sytsma, 1990; Donoghue & Sanderson, 1992; Doyle et al., 1994).

Incorporation of fossils is likely to be critical in cases of presumed rapid radiation in the distant past (Donoghue et al., 1989; Huelsenbeck, 1991b; Novacek, 1992). Fossils might represent more faithfully those character combinations that were present closer to the splitting events of interest. Their addition could, in effect, "shorten" the lengths of branches leading to extant taxa, thereby lessening the chance of spurious connections owing to chance convergences (the "long-branch attraction" problem; Felsenstein, 1978). Already there are examples of this effect (e.g., "progymnosperms" relative to seed plants), and the addition of recent paleobotanical discoveries (e.g., Crane et al., 1989; Pedersen et al., 1991; Cornet, 1986) could have a similar effect as regards angiosperms (Doyle & Donoghue, 1993).

METHODOLOGICAL ISSUES

Solving difficult phylogenetic problems will require additional evidence, but it will also depend on basic methodological advances. Thus, both the thought of combining data sets and the possibility of long-branch attractions highlight the need for more attention to taxon sampling for phylogenetic analysis (e.g., Donoghue & Sanderson, 1992; Wheeler, 1992; Kellogg & Watson, 1993). This is especially critical in view of the significant limitations of presently available computer algorithms in handling large numbers of taxa (Swofford & Olsen, 1990; Maddison, 1991; Maddison et al., 1992; Penny et al., 1992). Although there is some comfort in the extensive sampling of angiosperms in the Chase et al. (1993) analysis of 499 *rbc*L sequences, the results are correspondingly difficult to interpret. It is unclear whether all (or even any) of the most parsimonious trees actually have been recovered, and it is practically impossible to evaluate alternative hypotheses critically or to explore the robustness of the results using tests such as the bootstrap (Felsenstein, 1985; Sanderson, 1989) or decay analysis (Bremer, 1988; Donoghue et al., 1992). Of course, the same limitations apply to large morphological studies (e.g., Hufford, 1992; Kellogg & Watson, 1993).

In view of these problems, analyses involving large numbers of taxa must employ carefully designed (and explicit) search strategies to discover separate "islands" of parsimonious trees (Maddison, 1991; Maddison et al., 1992; Page, 1993b; Olmstead et al., 1993). Alternatively, there may be ways of reducing the number of taxa without sacrificing accuracy. One possibility, the use of a single "exemplar" species to represent a large clade, has the advantage of avoiding (at least partially) the problem of inferring basal states for the group in question. This strategy, however, entails its own risks. Most importantly, the inadvertent choice of an exemplar that is, in reality, nested well within the clade in question, might result in a mistaken estimate of the true relationships of the group. This could happen, for example, if the exemplar belonged to one specialized line within the group, which happened to have converged on another terminal taxon in the analysis.

A second option is the use of a "placeholder" for a number of terminal taxa, where there is evidence at the outset that these form a clade. In this case, some prior information on relationships within the group may make it possible to establish a set of ancestral conditions, by finding the most parsimonious character states at the basal node of the clade in question (algorithms are described by Swofford & Maddison, 1987). This approach, advocated by Mishler (1994) under the name "compartmentalization," has been used in morphological analyses for some time (though not always very explicitly). For example, Donoghue & Doyle (1989) performed a preliminary phylogenetic analysis within a presumably monophyletic core-Laurales clade and used the results to assign states to a placeholder for that line. Similarly, Doyle et al. (1994) used preliminary hypotheses on relationships within such groups as monocotyledons to "boil down" information on a set of observed terminal taxa to a set of ancestral state assignments. Fortunately, it may be sufficient to have only a partial prior hypothesis of relationships, as the states of taxa nested well within the clade in question may be effectively "screened-off" from having any effect on the assessment of basal conditions (Maddison et al., 1984).

The use of placeholders will mean that more than one character state will occur in some terminal taxa. An alternative approach, advocated by Nixon & Davis (1991), is always to subdivide polymorphic taxa into monomorphic terminal units. This, of course, can only aggravate the real-world problems posed by large numbers of taxa. Furthermore, subdivision based on the states of a character (one of which is presumably ancestral within the group) will result in para- or polyphyletic terminal units in many cases. For example, if angiosperms were subdivided into two terminal taxa based on the presence and absence of vessels it is highly likely that neither would be a clade. The same would be true of many other characters, such as the presence and absence of an active cambium, or different types of embryo sac development. Inclusion of nonmonophyletic terminal taxa in an analysis can result in erroneous conclusions about relationships and character evolution, at least if taxa are interpreted in the standard way, namely as representing real (single) branches of a phylogenetic tree.

In the end, the best method of coding large polymorphic taxa will depend on the circumstances. Sometimes it will be feasible and appropriate to split a polymorphic terminal unit into two or more groups (hopefully monophyletic), and this may not significantly increase the overall number of taxa. In other cases some form of compartmentalization will be possible, leaning cautiously on the results of previous analyses. The latter requires that the assumptions used in one analysis be vigorously tested in other, independent analyses, but such tests are certainly possible (e.g., Doyle et al., 1994). Another option is to simply code a terminal taxon as polymorphic, as can be done in PAUP (Swofford, 1993) and MacClade (Maddison & Maddison, 1992). In the case of multistate characters (such as nucleotides at a particular site) this need not be equivalent to coding the taxon as completely "unknown," since particular subsets of states can be specified. Although coding a taxon as unknown can sometimes have undesirable effects (Doyle & Donoghue, 1986; Nixon & Davis, 1991; Platnick et al., 1991), it may be necessary, especially to incorporate incomplete fossils (Maddison & Maddison, 1992).

Even in cases that continue to resist resolution, progress is made when relevant data and analyses are published, because, if nothing else, this clarifies the implications of alternative hypotheses. This is true, of course, only to the extent that sources of information (especially voucher specimens) are carefully documented, and only if the assumptions underlying the delimitation of taxa and characters are clearly spelled out. Phylogenetic research can be of lasting value only if all of the evidence underlying the results is made available for scrutiny. Otherwise, it is impossible to make reasoned choices among alternative hypotheses, or to learn anything at all from experience.

PROSPECTS

What can we look forward to over the next few years? Here I will briefly highlight what I believe to be several important trends and their likely consequences. At the base of each of these trends is a more fundamental shift to what O'Hara (1988) has called "tree-thinking": understanding diversity as the product of an underlying branching process, and observed differences as having resulted from evolutionary changes along the branches of a tree. That the shift away from a linear view of evolution is far from complete is evidenced by the language still so often used to describe evolutionary history, such as "lower" and "higher" in reference to taxa (O'Hara, 1992). Fortunately, however, tree-thinking is likely to figure more prominently in the curriculum, with software such as MacClade (Maddison & Maddison, 1992) making it easy and fun to explore the implications of evolutionary trees.

A PHYLOGENETIC SYSTEM

Although major changes will undoubtedly take time, I suspect that botanists will continue to move toward a truly phylogenetic system. By this I mean that taxa will be delimited so as to conform to our best estimates of phylogeny and will be defined in terms of ancestry rather than in terms of the characters used to diagnose them (Hennig, 1966; de Queiroz, 1988, 1992; Donoghue & Cantino, 1988; de Queiroz & Gauthier, 1992). In practical terms this will mean eliminating some familiar paraphyletic groups. An excellent example is provided by phylogenetic research on Asteraceae, culminating recently (Bremer et al., 1992) in several new names to reflect conclusions that are well supported by different sources of evidence (e.g., Barnadesioideae as the sister group of the rest of the family).

Many more changes of this sort will be made as our understanding of phylogeny improves. In particular, it is clear that some traditional angiosperm families are paraphyletic, with one or more monophyletic families nested within them. For example, Cantino (1992) has carefully documented the origin of several lines of Lamiaceae from within Verbenaceae. Judd et al. (1994) have documented similar situations in phylogenetic analyses of other presumably closely related families. In particular, Asclepiadaceae appear to be nested within a paraphyletic Apocynaceae, Apiaceae within Araliaceae, Brassicaceae within Capparaceae, Valerianaceae plus Dipsacaceae within Caprifoliaceae, Urticaceae within Moraceae, and Aceraceae and Hippocastanaceae within Sapindaceae. Many of these conclusions based on morphology are now also supported by molecular evidence (e.g., Chase et al., 1993). In most of these cases, we have proposed to eliminate paraphyly through recognition of a single more inclusive family (Judd et al., 1994). This, we hope, will help counteract a bias on the part of temperate botanists to segregate and elevate the rank of mainly temperate, mainly herbaceous groups, leaving behind a residue of woody tropical plants with which they are less familiar.

Although the shift to monophyly may entail rather major changes in some cases, this should hardly be viewed with dismay. Instead, such changes are a concrete sign that we are making progress in understanding phylogeny. Furthermore, although there will be resistance to changing traditional names, such changes are very likely to occur in the long run because a phylogenetic system is most useful in helping us understand evolutionary and ecological processes, biogeography, and so on (Hennig, 1966). Moreover, recognition of monophyletic groups makes it much easier to teach plant diversity and for students to learn about it. It also helps from the standpoint of continued analysis of phylogeny to have names for the clades we work with. The name "anthophyte," for example, has been useful in describing seed plant phylogeny. Likewise, we hope that the "stem-based" name "angiophyte" (Doyle & Donoghue, 1993) will facilitate discussion of how fossils such as *Sanmiguelia* (Cornet, 1986) relate to modern angiosperms.

In addition to better phylogenies, the development of a phylogenetic system requires attention to the logic of phylogenetic taxonomy and nomenclatural conventions. Here the analysis and recommendations of de Queiroz & Gauthier (1992) provide an excellent starting point. Among other things, I agree with them that we should seriously reconsider the need to designate standard Linnean ranks, especially in view of the evident temptation to treat taxa assigned to the same taxonomic rank as though they are somehow equivalent. Such rank-based approaches can lead, for instance, to systematic errors in studies of rates of extinction and diversification (Doyle & Donoghue, 1993).

PHYLOGENIES IN USE

The use of phylogenies by ecologists, paleontologists, biogeographers, molecular biologists, conservationists, and others will surely continue to increase (e.g., Brooks & McLennan, 1991; Harvey & Pagel, 1991). In the case of angiosperms, for example, the availability of trees has already had an impact on studies of a wide variety of characters, including vessels (Young, 1981; Donoghue & Doyle, 1989), dioecy (Donoghue, 1989), double fertilization and endosperm (Donoghue, 1989; Freidman, 1992; Donoghue & Scheiner, 1992), pollen morphology (Doyle & Hotton, 1991), pollination (Pellmyr, 1992), and self-incompatibility (Weller et al., 1994). Many other ideas on the direction of morphological evolution (discussed, for example, by Stebbins, 1974; Carlquist, 1975; Cronquist, 1988; Takhtajan, 1991) will soon be tested in a phylogenetic context. Similarly, phylogenies will have an increasing impact on our understanding of molecular evolution. For instance, we can look forward to a fruitful period of "reciprocal illumination" between studies of plant phylogeny and molecular genetic analyses of the mechanisms underlying flower development (Coen & Meyerowitz, 1991).

The use of phylogenies in other studies will force phylogenetic systematists to attend to the issue of reliability. Quite naturally, those who intend to rely on phylogenies will want some indication as to how believable they are. A variety of methods have been developed (e.g., Felsenstein, 1985; Bremer, 1988; Sanderson, 1989; Archie, 1989; Hillis, 1991; Huelsenbeck, 1991a; Goloboff, 1991a; Faith, 1991; Donoghue et al., 1992) and there is a growing (mostly critical) literature on the logic and behavior of such methods (e.g., Carpenter, 1992; Goloboff, 1991b; Kallersjo et al., 1992; Hillis & Bull, 1993). Here it will be critical to develop a deeper understanding of the underlying philosophical and statistical issues. If it emerges that particular methods are unsatisfactory, then it behooves us to articulate exactly why this is the case and then to develop and test better methods. In the meantime, users of trees should be warned of uncertainties and encouraged to take into account ambiguities in estimates of the phylogeny and of character change (e.g., Maddison, 1991; Maddison et al., 1992; Weller et al., in press).

Progress in assessing confidence will require a better understanding of possible sources of error, such as long-branch attraction (e.g., Albert et al., 1994). In particular, we need to know more precisely how to distinguish real signal from spurious results. Despite their limitations (Hillis et al., 1992), computer simulations will continue to be a useful approach to such questions, making it possible to explore a very wide range of possible parameter values (e.g., Lanyon, 1988; Huelsenbeck & Hillis, 1993; Kim et al., 1993). Of course, such studies leave open the critical question of exactly where in parameter space any particular problem is situated, but it is nevertheless important to formalize the universe of possibilities and the impact of critical variables.

Work with known phylogenies (e.g., Atchley & Fitch, 1991; Hillis et al., 1992) and experimentation with real data sets (e.g., Smith, 1989; Donoghue et al., 1989; Allard & Miyamoto, 1992) also will be useful. An approach that deserves more attention is the use of random nucleotide sequences as benchmarks to help determine whether real sequences have retained signal relative to a particular phylogenetic problem (e.g., Miyamoto and Boyle, 1989; Wheeler, 1990; Maddison et al., 1992). For example, David Maddison and I (unpublished analysis) are using this approach to evaluate the attachment of real outgroup sequences to the *Ceratophyllum* branch in angiosperm trees based on *rbc*L data (Les et al., 1991; Chase et al., 1993). Is this the true position of the root, or are real outgroup sequences so highly diverged that, in effect, they no longer retain phylogenetic information? Our preliminary studies show that most "random" sequences (generated under several models) also attach to the "long" *Ceratophyllum* branch. Nevertheless, there are some aspects of the behavior of real outgroup sequences that deviate from any of the random sequences we have investigated, implying that the real sequences may not be entirely devoid of phylogenetic signal. More experiments are needed, as are more sensitive statistical tests.

Increased interest in phylogenies also demands that we develop better ways of making information about them accessible to potential users. We need, in short, to assemble a database of phylogenetic data and trees (Sanderson et al., 1993). At the same time, we should establish standard means for depositing phylogenetic data as a co-requisite of publication, just as nucleotide sequences are now routinely transmitted electronically to repositories such as Genbank (Cinkosky et al., 1991). On a practical level, such a database would allow systematists to respond rapidly to requests for phylogenetic information in connection, for example, with conservation efforts (e.g., Vane-Wright et al., 1991). Moreover, accessibility of the full range of phylogenetic studies surely would facilitate the search for general patterns; for example, patterns in levels of homoplasy (e.g., Sanderson & Donoghue, 1989), or in tree shape (e.g., Savage, 1983; Guyer & Slowinski, 1991, 1993). It would also revolutionize the search for general patterns in geographic distributions, by allowing (at least potentially) ready access to every tree with taxa present in particular areas of endemism (e.g., Nelson & Platnick, 1981; Page, 1991).

PHYLOGENIES AND POPULATION BIOLOGY

Systematics is sometimes portrayed as being neatly separated from population biology, and it is sometimes implied that this gap should be maintained (e.g., Nixon & Wheeler, 1990). This, I believe, is a mistake. On the contrary, interactions with population biologists should be promoted actively. Such contacts promise to be especially fruitful in view of obvious mutual concerns centered on the analysis of gene trees and the recent emergence of coalescence theory (Pamilo & Nei, 1988; Avise, 1989; Takahata, 1989; Hudson, 1990; Doyle, 1992; Page, 1993a; Baum & Shaw, in press; Maddison, in press).

The application of phylogenetic methods to what have traditionally been population-level problems is yielding promising results already. For example, Slatkin & Maddison (1990) devised a phylogenetic measure of gene flow, and Felsenstein (1992) has approached the estimation of effective population size from a phylogenetic standpoint. It is perhaps less obvious how systematists, especially those of us primarily concerned with deeper branching events, stand to benefit from interacting with population biologists. However, several fundamental questions require population-level input. One such concern is the possibility of a false estimate of phylogeny based on uniparentally inherited organellar DNA (e.g., Rieseberg & Soltis, 1991; Doyle, 1992). Whether lineage sorting, for example, is likely to have been an important factor in a particular case depends on population sizes and the time intervals between splitting events. We recognize that these are the important parameters, and we know something about their critical values, based on models developed by population geneticists (e.g., Pamilo & Nei, 1988; see Maddison, in press). Moreover, population biologists may be able to estimate these parameters in particular cases. Ultimately, this could bear directly on the way in which organellar data are integrated with other evidence in phylogenetic analysis (Doyle, 1992).

Input from population geneticists also will be critical in understanding processes such as concerted evolution and the dynamics underlying the establishment of paralogous genes, issues of obvious interest to molecular systematists (e.g., Zimmer et al., 1980; Patterson, 1988; Sanderson & Doyle, 1992). Better understanding of these phenomena will help guard against mistaken comparisons, and will allow us to turn them to our advantage in some cases. For example, comparison of phylogenies based on paralogous genes may make it possible to establish the root of a tree. In fact, this approach allowed Iwabe et al. (1989) to root the tree of life, despite the lack of obvious outgroups.

The ability to compare trees based on both nuclear and organellar genes obviously has expanded our ability to identify hybrids and specify their parentage (e.g., Soltis et al., 1989; Rieseberg & Brunsfeld, 1992). Although hybrids have occasionally been discussed by phylogeneticists (papers in Platnick & Funk, 1983; Funk, 1985), detailed empirical studies of their impact on phylogeny reconstruction have appeared only recently (McDade, 1992). Nevertheless, botanists should soon play a major role in developing methods for the recognition and incorporation of reticulations in phylogenetic analysis (e.g., Rieseberg & Morefield, in press). Ultimately, what is needed is a general theory covering reticulations of all sorts (Page, 1993a), including recombination in the case of genes (Hein, 1990), lateral transfer of DNA (Valdez & Piñero, 1992), and even the fusion of entire biotas in biogeography (Cracraft, 1988). The development of such a theory depends on breaking down whatever barriers have tended to separate population biologists from systematists.

SUMMARY

It seems clear that headway has been made in understanding plant phylogeny over the last few decades, and there is every reason to expect continued success. It is also clear, however, that many basic phylogenetic questions will be rather difficult to answer. New morphological and molecular evidence, in combination with the old, should eventually point the way to a solution. At the same time, methodological advances will allow us to get more mileage out of whatever data are available.

Better phylogenies will lead (hopefully) to taxonomic changes, and will surely encourage the use of trees outside of systematics. One result will be increased attention to problems of taxon sampling and to methods for assessing the reliability of phylogenetic hypotheses. Eventually, we will see the development of an even more comprehensive phylogenetic theory, incorporating reticulation of all kinds and transcending the boundaries of traditional disciplines.

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