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Phylogenies and angiosperm diversification

James A. Doyle and Michael J. Donoghue

Abstract.—Approaches to patterns of diversification based on counting taxa at a given rank can be misleading, even when all taxa are monophyletic. Such “rank-based” approaches are unable to reflect a hierarchy of evolutionary events because taxa of the same rank cannot be nested within one another. Phylogenetic trees specify an order of origination of characters and clades and can therefore be used in some cases to test hypotheses on causal relationships between characters and changes in diversity. “Tree-thinking” also clarifies discussions of the age of groups, by distinguishing between splitting of the stem-lineage from its sister group and splitting of the crown-group into extant clades.

Cladistic evidence that *Pentoxylon*, Bennettitales, and Gnetales are the sister group of angiosperms implies that the angiosperm line (angiosphytes) existed by the Late Triassic. The presence of primitive members of five basic angiosperm clades indicates that the crown-group (angiosperms) had begun to diversify by the mid-Early Cretaceous (Barremian–Aptian), but not necessarily much earlier. The greatest unresolved issue raised by cladistic analyses concerns the fact that the angiosperm tree can be rooted in two almost equally parsimonious positions. Trees rooted near Magnoliales (among “woody magnoliids”) suggest that the angiosperm radiation may have been triggered by the origin of intrinsic traits, e.g., a fast-growing, rhizomatous habit in the paleoherb and eudicot subgroup. However, trees rooted among paleoherbs, which are favored by rRNA data, imply that these traits are basic for angiosperms as a whole. This could mean that the crown-group originated not long before its radiation, or, if it did originate earlier, that its radiation was delayed due to extrinsic factors. Such factors could be a trend from environmental homogeneity and stability in the Jurassic to renewed tectonic activity and disturbance in the Early Cretaceous. Potentially relevant pre-Cretaceous fossils cannot be placed with confidence, but may be located along the stem-lineage (stem angiosphytes); their generally paleoherb-like features favor the paleoherb rooting. The history of angiosphytes may parallel that of Gnetales: some diversification of the stem-lineage in the Late Triassic, near disappearance in the Jurassic, and vigorous radiation of the crown-group in the Early Cretaceous.

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Introduction

Despite increasing interest in the use of phylogenetic trees in evolutionary biology, our impression is that “tree-thinking” (O’Hara 1988) has not yet had the impact that it could have in studies of rates of evolution and biotic turnover. Our aim is to promote a phylogenetic approach by illustrating the value of trees in studying the origin and radiation of a major group, the angiosperms (flowering plants). In view of continued uncertainties regarding angiosperm phylogeny, this example also shows how different phylogenetic hypotheses can have rather different implications, and how formulating the problem in terms of trees may be useful even in the absence of a single well-supported phylogeny.

This analysis goes beyond previous discussions by ourselves and others in exploring in depth the implications of cladograms concerning the prehistory of the angiosperm line, before its main radiation in the Early Cretaceous, and the impact of recent molecular analyses and discoveries of pre-Cretaceous fossils.

Ranks versus Trees.—Studies of changes in diversity have often relied heavily on the taxonomic literature (e.g., Sepkoski 1978; Valentine 1985). In particular, it is commonplace to count the number of taxa of a given taxonomic rank (genera, families, etc.) at particular time periods, and then to examine changes in these numbers to identify episodes of extinction and radiation. Problems

with the use of such "rank-based" approaches in studies of the adaptive significance of characters are now widely appreciated (Felsenstein 1985; Donoghue 1989), and a variety of phylogenetic approaches to such questions have been developed (Brooks and McLennan 1991; Harvey and Pagel 1991). Before turning to the angiosperm question, we wish to clarify, in general terms, why we think tree-based approaches are preferable to those based on taxonomic ranks. Here we concentrate on analyses based on supraspecific taxa; for some purposes it might theoretically be possible to reduce the problems by going to the species level, but this would not help in other cases.

A common concern is that taxa assigned to the same rank may not be comparable in any way that is relevant to the problem at hand, and that rank-based results may reflect aspects of taxonomic practice and tradition rather than genuine evolutionary patterns (Eldredge and Cracraft 1980; Cracraft 1981; Smith and Patterson 1988). For example, families are not necessarily of the same age, nor do they encompass the same amount of diversity when measured in terms of either species richness or degree of morphological divergence. Phylogenetic systematists have drawn attention to the fact that taxa also may not be comparable in how they reflect common ancestry. Some traditional taxa are monophyletic (i.e., comprised of an ancestor and all of its descendants), but others are paraphyletic (i.e., comprised of an ancestor and only some of its descendants). This difference may be highly significant in studies of biotic turnover. For example, "extinction" has a different meaning for monophyletic and paraphyletic groups (Hennig 1966): the "true" (complete) extinction of monophyletic taxa must be distinguished from the "pseudoextinction" of paraphyletic taxa, wherein some descendants of the common ancestor are still living (Patterson and Smith 1987).

Paraphyly seems to be widely viewed as *the* cladistic challenge to rank-based studies in paleobiology, and efforts have therefore been made to side-step the basic arguments against paraphyly (e.g., Sepkoski 1987). This seems to assume that if there were some way to take care of the paraphyly problem, it would be

valid to proceed with a rank-based approach. We will argue that this view is misguided. Although paraphyly certainly is responsible for many difficulties, rank-based approaches suffer from an even more basic weakness.

The pitfalls of paraphyly have been most widely explored in studies of character evolution, which have often attempted to infer causal connections from statistical associations of different traits (Felsenstein 1985; Donoghue 1989). If the number of occurrences of a trait in taxa of a given rank is used to estimate the minimum number of times the trait evolved, inclusion of paraphyletic taxa may lead to errors. For example (fig. 1), if a derived trait of a paraphyletic group (A) was retained by the group nested within ("derived from") it (B), the trait might be scored as having evolved twice. Although a correct estimate might be obtained by recognizing one monophyletic group at the rank in question that happened to include all the descendants of the ancestor in which the trait evolved (C), breaking up this group into several monophyletic groups (D, E, and F) would again result in an overestimate. Reversals can lead to further misestimates. The general reason why counting taxa of a given rank cannot give an accurate reflection of character evolution, whether the taxa are paraphyletic or monophyletic, is straightforward. Studies of character evolution are necessarily concerned with a sequence of events: first A evolved, then B evolved from A, and so on. This information cannot be captured by reference to any one rank, no matter how well the overall classification reflects the underlying tree. This is because taxa of the same rank cannot be nested within one another, and they therefore cannot reflect the hierarchy of evolutionary events inherent in the phylogeny.

The same problems hamper rank-based estimates of rates of extinction. Inspection of the tree in figure 2 shows that there are extant descendants of the interior nodes numbered 1–4, but the three branches represented by interior nodes 5–7 are extinct (e.g., derivatives of node 4 might be birds, the rest "dinosaurs"). These simple observations cannot be reflected in a count of taxa. Use of paraphyletic groups might lead to one sort of er-

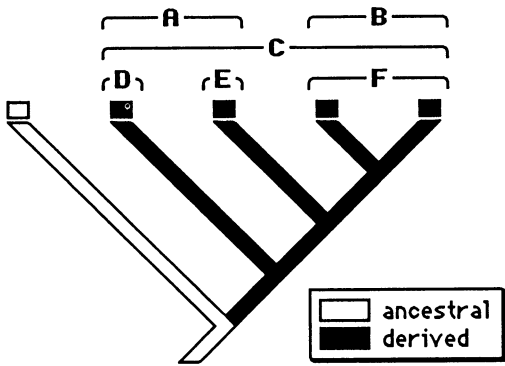


FIGURE 1. Limitations of a rank-based approach to character evolution. Inclusion of paraphyletic groups (A) can lead to an overestimate of the number of times a trait evolved, but so can classifications containing only monophyletic groups (e.g., D–F).

ror. Recognizing taxa A and B, one of which is paraphyletic, would suggest that one group went extinct and the other survived. However, this is misleading. First, it gives the impression that there are no living descendants of anything in taxon A, which is false because nodes 1–3 do have descendants, namely those that happen to have been placed in B. This is the pseudoextinction problem mentioned above (Patterson and Smith 1987). Second, it fails to reflect the fact that three separate branches (5–7) went extinct. These problems cannot be overcome by eliminating paraphyletic groups. Inclusion of all these groups in one taxon at the rank under consideration would imply that there was no extinction, but this would obscure the obvious fact that lines 5–7 all died out (like implications that K–T “dinosaur” extinctions were insignificant because birds are still extant). Another delimitation of monophyletic groups, C and D, would again lead to the conclusion that one group went extinct and the other did not. While this eliminates the pseudoextinction problem, it still fails to reflect the fact that lines 6 and 7 also went extinct. Even the delimitation of monophyletic groups E–H is insufficient. Here a count of taxa accurately reflects the fate of nodes 4–7, but it fails to capture the fates of nodes 1–3.

This example implies that the number of extinctions and survivals of lineages cannot be accurately and completely reflected by tallying the number of taxa of a given rank,

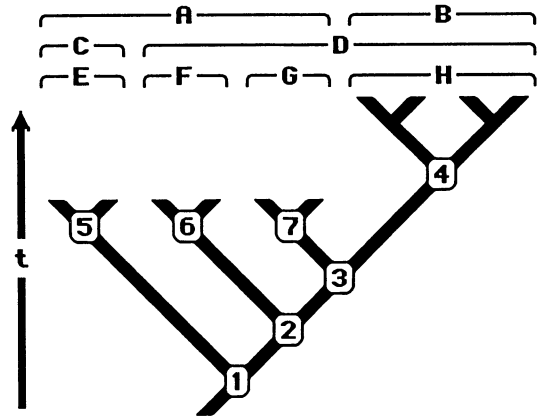


FIGURE 2. Limitations of a rank-based approach to extinction. Inclusion of paraphyletic groups (A) can lead to an incorrect estimate of the number of lines that went extinct, but so can classifications containing only monophyletic groups (e.g., C–D, or even E–H: see text).

whether or not any groups are paraphyletic. Again, reliance on taxa that cannot be nested within one another prevents recognition of the sequence of evolutionary events. In principle, a rank-based approach might be salvaged by simultaneous reference to taxa at several different ranks. However, the success of this approach would depend on knowledge of the underlying tree. And when such information is available there is no need to make use of taxa; instead, the quantities of interest (number of origins of a trait, number of extinctions, etc.) can be inferred directly by inspection of the tree.

Rank-based approaches also lead to problems in studying rates of diversification (Cracraft 1981; Novacek and Norell 1982). Since taxa of the same rank are not necessarily of the same age, comparison of the number of species can be misleading. For example, the rate of speciation and extinction might be the same in two families, but the absolute number of species could be very different simply because one is much older than the other. Inclusion of paraphyletic taxa could also lead to errors as a result of omitting descendant species that happen to have been placed in a different taxon.

One proposed solution to these problems, which relies on some knowledge of phylogeny, is to confine comparisons of species numbers to sister groups (e.g., Vrba 1980; Cra-

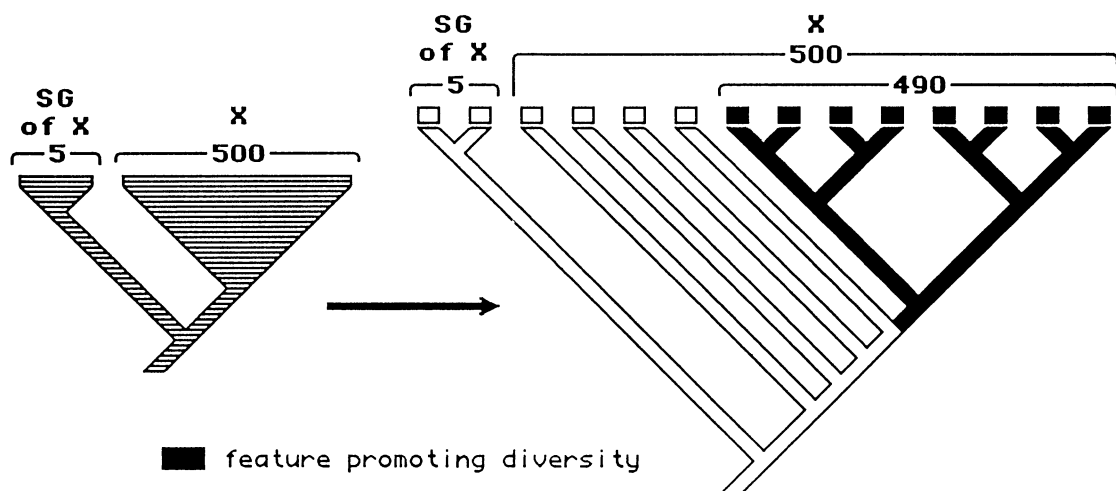


FIGURE 3. Limitations of a rank-based approach to diversification (sister group comparison). The greater diversity of X than its sister group (SG) may be the result not of a trait that originated in the ancestor of X, but rather of a trait of one clade within X.

craft 1984; Slowinski and Guyer 1989; Farrell et al. 1991). If the two groups are correctly assessed as monophyletic, they must be the same age, since their origin traces to the same event, the splitting of their common ancestor. Furthermore, monophyly insures that, in principle, no descendant species have been excluded (in practice, extinct species might not be counted). Although this is a step in the right direction, it can still be misleading for the same reason noted previously. Reducing the comparison to taxa that cannot be nested within one another effectively hides information on the sequence of events within and outside of the groups in question, which could be ascertained from a more complete phylogeny. This might be critical in determining where and why there were shifts in diversification rates.

This point is illustrated in figure 3. Clade X (perhaps a family) is observed to be far more diverse (with 500 species) than its sister group (a family with five species). A simple comparison of the number of species in the two groups might suggest that the disparity was a function of some attribute of family X that resulted in a higher rate of diversification, perhaps a "key innovation" that evolved along the branch subtending X. However, more complete information on phylogenetic relationships within the two groups, specif-

ically the observation of a series of early branches that are not especially diverse followed by a diverse clade in which branching is more or less equal on both sides of each split, might suggest instead that the change in diversification rate actually occurred at the base of the diverse clade nested within X. This might in turn suggest that the greater total diversity of X is the consequence of a character or characters that evolved within X, rather than at its base (e.g., see Raikow 1988; Crane and Lidgard 1990).

This example shows that rank-based approaches to estimating rates of diversification can be misleading even when all taxa under consideration are monophyletic. It also implies that it is sometimes possible to infer where there have been shifts in diversification rate by reference to tree topology alone. In fact, Sanderson and Bharathan (in press) provide a method for doing this, which associates rates of cladogenesis with particular branches of a tree and minimizes such changes in a manner analogous to parsimony optimization. In other cases, stratigraphic information may also be needed, and we certainly agree with Sanderson and Bharathan that the best inferences will take into account both tree topology and stratigraphic evidence. The main message of Sanderson and Bharathan's analysis, and of our figure 3, is simply that

knowledge of phylogeny can have an impact on our understanding of diversification rates. Thus, trees can modify a view of diversification based solely on the comparison of taxonomic diversity at different time periods, or even a view based on comparing the numbers of species in sister groups. It is this realization that motivates our reevaluation of the timing of angiosperm diversification.

This is not to say that all results of rank-based approaches are wrong: such approaches may often yield a more or less accurate picture of underlying patterns, just as phenetic analyses often yield the same groupings as phylogenetic ones. It may be possible to get the right result with the wrong tool, but this is no excuse for not using the right tool when it is available. The problem is that it is unclear whether the right results have been obtained in any particular case in the absence of phylogenetic information.

We also recognize that it is easier to advocate tree-based approaches than it is to implement them. Trees are unavailable for many groups, and those that are available are often poorly resolved or inaccurate. Furthermore, even when robust estimates can be obtained, there are difficulties at other stages of the analysis, such as optimization (mapping) of character state changes on trees. These are genuine difficulties in practice, but they are not fundamental structural problems; they can be overcome as we learn more about relationships. In the meantime, efforts to develop and apply methods that are at least cognizant of an underlying phylogeny (e.g., Gilinsky 1991; Gilinsky and Good 1991), or those that focus on particular sister group comparisons or other aspects of tree topology (e.g., Slowinski and Guyer 1989; Guyer and Slowinski 1991) should certainly be encouraged. These, we suggest, are more promising than attempts to salvage rank-based approaches, which seem fundamentally unsatisfactory for evolutionary studies. In the long run, we look forward both to improved understanding of phylogeny and to the development of methods that take full advantage of this understanding.

Cladograms and Ages of Groups.—As noted by Hennig (1965), any extant group can be

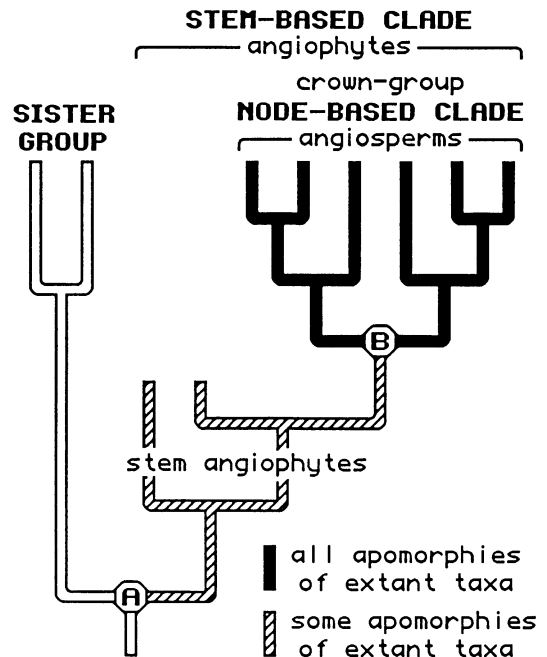


FIGURE 4. Distinction between two ages of group X, defined by nodes A and B, and between stem- and node-based taxa.

considered to have at least two ages, which may be greatly separated in time. The first is the date that the line including the group split from its extant sister group (node A in fig. 4), the second is the date that the line first split into extant subgroups (node B). A third sort of age is the date of origin of a particular apomorphy of the group, which should usually lie somewhere between nodes A and B. Corresponding to this distinction, names in the phylogenetic system can be applied to the whole lineage above node A, to node B and its derivatives, or to derivatives of the first ancestor that possessed a particular apomorphy (i.e., stem-based, node-based, and apomorphy-based in the terminology of de Queiroz and Gauthier 1990).

In discussing the relationships of fossils to extant groups, Hennig (1969) and Jefferies (1979) distinguished between the "crown-group," which includes node B and its derivatives, and the "stem-group," which includes all forms between nodes A and B, whether directly on the line to the extant group (i.e., the stem-lineage) or on extinct side-branches. In terms of characters, crown-group forms are

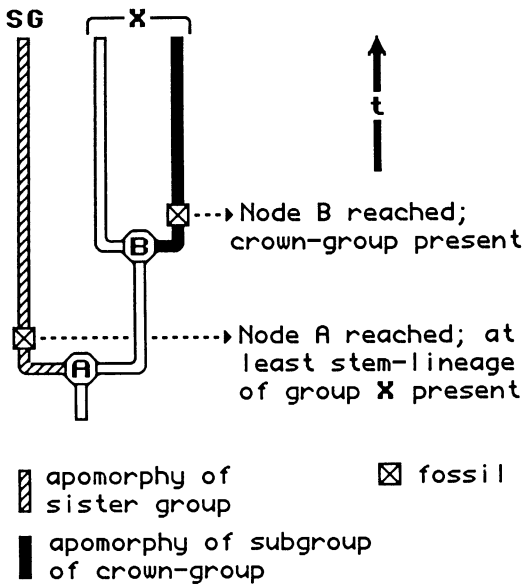


FIGURE 5. A fossil with apomorphies of the sister group of X implies that the stem-lineage of X was in existence even in the absence of fossils of X itself. A fossil with apomorphies of a subgroup of X implies that the crown-group had begun to diversify.

expected to have all of the synapomorphies that characterize extant members (excluding parallelisms or losses), whereas stem-group forms should have some of these advances but not others. However, the term “stem-group” has been criticized because it suggests the presence of a valid phylogenetic group, whereas such a group would obviously be paraphyletic (Ax 1985). This problem can be avoided by using one name for the crown-group (a node-based name) and another (a stem-based name) for the more inclusive clade containing the crown-group and its extinct relatives (de Queiroz and Gauthier 1990, 1992).

Theoretically, an established name like “angiosperms” could be defined in stem-based, node-based, or apomorphy-based terms. However, de Queiroz and Gauthier (1992) have argued that it is best to use such names for node-based taxa (crown clades) and to propose new names for the corresponding stem-based taxa (e.g., Ornithosuchia for the clade including birds and “dinosaurs,” above their common ancestor with crocodiles). Other definitions invite incorrect assumptions that fossil taxa assigned to the group had the whole suite of apomorphies diagnostic for the

better-known extant members. This logic is particularly appropriate for angiosperms. Because angiosperms are separated from other seed plants by a very large number of apomorphies (see below), a stem-based definition would include forms much more primitive than any of the modern angiosperms, possibly lacking their most familiar features. A definition based on an apomorphy such as the carpel, although most consistent with the etymology of the name (“vessel seeds”), might be equally misleading, because it is not known whether the carpel arose early or late relative to other features associated with angiosperms. Thus we will henceforth restrict the term “angiosperms” to the crown-group. For the whole stem-based taxon above node A, we propose the term “angiophytes,” which we will sometimes refer to as “the angiosperm line.” In other cases where more is known from the fossil record about the sequence of origin of features, an apomorphy-based name might be more appropriate (e.g., defining “seed plants” to include well-known fossils like *Lyginopteris* and *Medullosa* that attach below the common ancestor of extant forms: Doyle and Donoghue 1986, 1992).

This terminology is still not wholly satisfying, since it does not provide a way to specify whether a particular fossil taxon is located between nodes A and B or in the crown-group, except by cumbersome expressions like “non-angiosperm angiophyte.” This is often a crucial question when discussing the significance of fossil forms. As a solution, we will use the term “stem” alone as a modifier (“stem angiophytes”) to designate forms between nodes A and B, with the understanding that these do not form a clade. In other cases where we have not proposed a stem-based name, we will use the expression “stem relatives of” the extant group.

The key to using trees to estimate the age of nodes A and B is the principle that sister lineages are of equal age (fig. 5). Even in the absence of actual fossils of group X, evidence for its sister group at a particular stratigraphic level (i.e., a fossil with apomorphies of the sister group) implies that node A had been reached and at least the stem-lineage of X existed at the same time. Evidence for more

than one extant subgroup of X, which can be the presence of just one subgroup if it has apomorphies that arose within the crown-group, implies that node B had been reached. These estimates are of course minimum ages. A fossil with crown-group apomorphies in all its available characters but with no apomorphies of any subgroup is a potential member of the crown-group, but confidence that it belongs above node B depends on how completely its various organs and characters are known.

It must be emphasized that this reasoning requires that all groups under consideration be monophyletic (fig. 6). For example, if it is assumed that groups X and Y are monophyletic sister groups (fig. 6a), presence of an early representative of Y might give one estimate for the age of node A. However, if Y is actually a paraphyletic group that X is nested within (fig. 6b), node A could be much younger, nearer the age of the oldest fossil of the true sister group of X, Z.

Evidence on the Age of Angiophytes and Angiosperms

Before exploring how trees can orient studies of angiosperm diversification, we first consider what the fossil record and phylogenetic analyses imply about the age of nodes A and B.

Angiophytes (Node A).—The most important recent insights into the age of node A come from analyses of the position of angiosperms in the phylogeny of seed plants as a whole (Crane 1985; Doyle and Donoghue 1986, 1992; fig. 7), including major lines of Recent and fossil "gymnosperms" (=non-angiospermous seed plants). These analyses agree that angiosperms are most closely related to Mesozoic *Pentoxylon* and Bennettitales and Recent Gnetales; the four groups together have been designated anthophytes because they all have flower-like reproductive structures made up of closely aggregated sporophylls (pollen- and/or seed-bearing appendages). Anthophytes are in turn nested among so-called Mesozoic seed ferns, implying a shift from fern-like pinnately compound leaves and sporophylls to a simple though still pinnately organized type. Angiosperms are linked di-

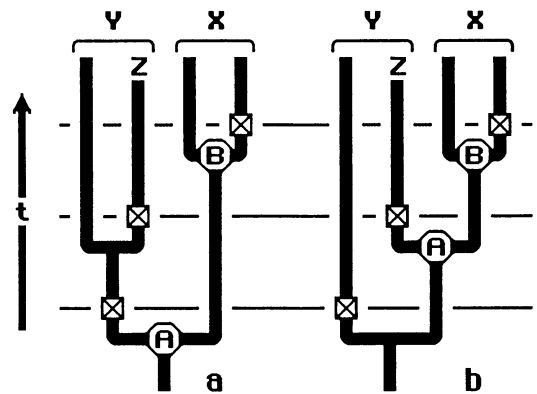


FIGURE 6. Dependence of age estimates on correct assessment of monophyly. Given the fossil occurrences indicated, the assumption that X and Y are monophyletic sister groups implies that the line leading to X is more ancient than it is if Y is paraphyletic and the true sister group of X is Z.

rectly with Gnetales in the trees of Crane (1985), but they are the sister group of all other anthophytes in the trees of Doyle and Donoghue (1986, 1992). This difference is due largely to Crane's assumption that several similarities of angiosperms and Gnetales that are not preserved in fossils were absent in *Pentoxylon* and Bennettitales. When these characters are scored as unknown in the fossils (as we believe they must be), the relationships shown in figure 7 are favored by advances shared by *Pentoxylon*, Bennettitales, and Gnetales, such as reduced sporophylls with one orthotropous ovule, whorled microsporophylls, and a tubular micropyle. In either case, Gnetales are the closest living relatives of angiosperms, as also inferred from analyses of extant plants alone (Doyle and Donoghue 1987; Loconte and Stevenson 1990; Hamby and Zimmer 1992).

What these results imply about the age of angiophytes can be seen by considering the fossil record of their presumed sister group—*Pentoxylon*, Bennettitales, and Gnetales (fig. 8). The best-known occurrences of *Pentoxylon*, including the Indian type material originally considered Jurassic, are now dated as Early Cretaceous, but putatively related fossils extend to the Early Jurassic of Australia (Drinnan and Chambers 1985). Numerous foliar and reproductive remains of Bennettitales are known from the Late Triassic onward (Crane

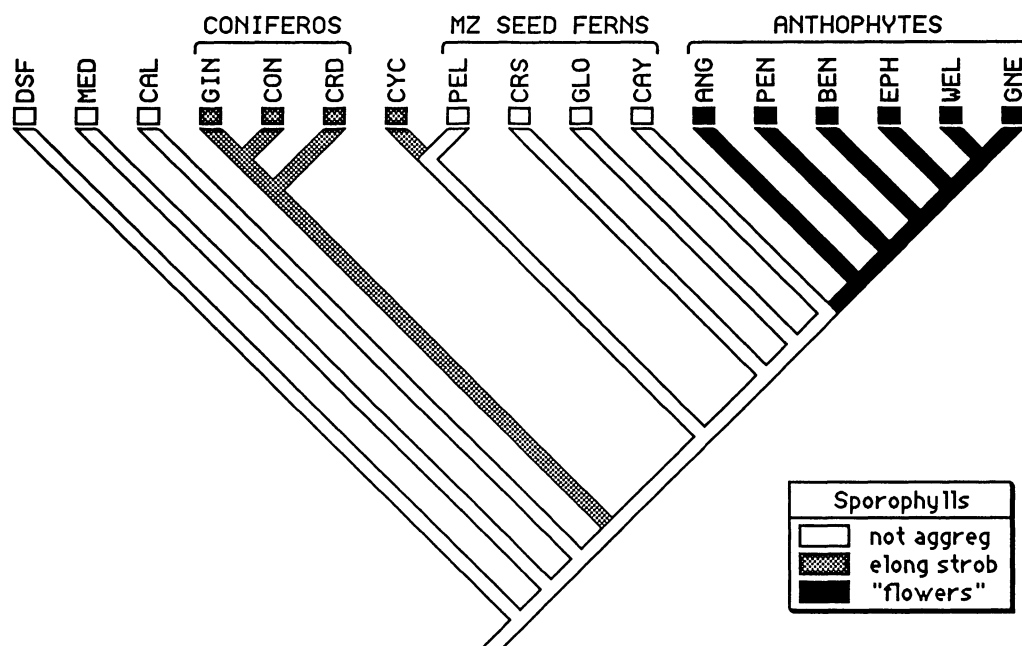


FIGURE 7. Representative most parsimonious cladogram of seed plants (Doyle and Donoghue 1992). DSF, Devonian protostelic "seed ferns"; MED, Medullosaceae; CAL, *Callistophyton*; GIN, Ginkgoales; CON, Coniferales; CRD, Cordaitales; CYC, Cycadales; PEL, *Peltaspermum*; CRS, Corystospermaceae; GLO, Glossopteridales; CAY, Caytoniaceae; ANG, angiosperms; PEN, *Pentoxylon*; BEN, Bennettitales; EPH, *Ephedra*; WEL, *Welwitschia*; GNE, *Gnetum*; CONIFEROS, coniferopsids. Branch shading illustrates the conclusion that the "flowers" of angiosperms and the elongate strobili of coniferopsids and cycads originated independently from less strongly aggregated sporophylls; this character was not used in the original analysis.

1988). Gnetales first become abundant in the Early Cretaceous, represented by dispersed "ephedroid" pollen with striate sculpture (Trevisan 1980; Doyle et al. 1982; Crane and Lidgard 1989) and by recently described vegetative and reproductive remains (*Eoantha*: Krassilov 1986; *Drewria*: Crane and Upchurch 1987; Pons et al. 1992). These appear to be crown-group forms: the spectrum of pollen types includes and extends beyond the morphological range of *Ephedra* and *Welwitschia* (*Gnetum* has more derived and less diagnostic inaperturate pollen), *Eoantha* is not more primitive than extant Gnetales in any available characters, *Drewria* has cross-veins and subepidermal fibers linking it with the subgroup made up of *Welwitschia* and *Gnetum*, and the Brazilian fossils of Pons et al. share derived features with either *Ephedra* or *Welwitschia*. However, less abundant ephedroid pollen extends to the Late Triassic. This has been associated with the macrofossil *Dechellyia*, which has enigmatic reproductive struc-

tures not readily comparable with the compound strobili of Recent Gnetales and was originally interpreted by Ash (1972) as a conifer, but which has opposite, linear leaves consistent with a relationship with Gnetales (Crane 1988). Wood with "herringbone" multiseriate rays like those of *Ephedra*, though without the vessels characteristic of all Recent Gnetales, occurs in the same formation (*Schilderia*: Daugherty 1934). The combination of gnetalian apomorphies and more plesiomorphic features in both *Schilderia* and *Dechellyia* suggest that these Triassic forms (and Early Jurassic fossils described by van Koenigseburg-van Cittert 1992) were located along the gnetalian stem-lineage. However, the implications for the age of angiosperms are the same.

It is interesting to note that Bennettitales and Gnetales are examples of the large number of plant groups that appeared and proliferated in the Late Triassic, others being the fern families Matoniaceae and Dipteridaceae,

crown-group Cycadales, definite Ginkgoales and related Czekanowskiales, and the extinct conifer family Cheirolepidiaceae. These appearances are associated with recovery from the arid conditions that dominated lower latitude regions in the Permian and earlier Triassic (Vakhrameev 1970).

If the relationships in figure 7 are correct, and if all the relevant groups are monophyletic (an assumption supported by several apomorphies of each group: Doyle and Donoghue 1986), these observations imply that angiosperms were distinct as far back as the Late Triassic. This constitutes a minimum age for node A. The same result is obtained if Gnetales are assumed to be the sister group of angiosperms (Crane 1985).

Angiosperms (Node B).—This last conclusion may seem disconcerting, or even a step backward, to those familiar with the history of paleobotanical views on the subject. It was originally thought that angiosperms were differentiated into advanced modern families at their first generally accepted appearance in the Early Cretaceous (Darwin's "abominable mystery"), which led to the inference that they had a long, hidden pre-Cretaceous history in some isolated area such as the tropical uplands (Axelrod 1952, 1970). However, beginning in the 1960s, studies of Cretaceous angiosperm pollen and leaves revealed a stratophenetic pattern that is hard to explain except in terms of a rapid radiation: a steady increase in species numbers, a stepwise increase in the spectrum of morphological types, and stratigraphic trends consistent with those inferred from comparative studies of modern angiosperms (Doyle 1969, 1977; Muller 1970; Doyle and Hickey 1976; Hickey and Doyle 1977; Crane and Lidgard 1990). The oldest unquestioned angiosperm pollen grains (recently extended from the Barremian to the Hauterivian or Valanginian: Brenner and Crepet 1986; Hughes and McDougall 1987; Trevisan 1988) are monosulcate, and these are joined in succession by tricolpates (late Barremian–Aptian), tricolporates (late Albian), and tripates (Cenomanian) (see table 1 for time scale). The oldest leaves (Aptian) are simple and have irregular, disorganized venation; these are followed by lobate and com-

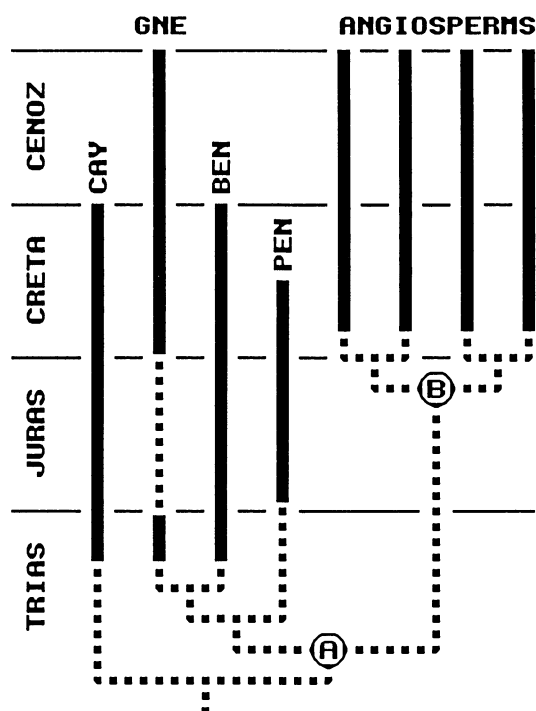


FIGURE 8. Stratigraphic ranges of the closest relatives of angiosperms, based on figure 7, and their implications for the age of node A (angiosperms). Abbreviations of taxa as in figure 7, except GNE, Gnetales.

pound types with more regular venation (Albian). Discoveries of fossil flowers have allowed more precise systematic comparisons (Friis and Crepet 1987; Friis and Crane 1989; Taylor and Hickey 1990), but their record begins too late (only a few poorly understood forms before the Albian) and is not yet dense enough for strong generalizations about trends.

The critical point is that these observations relate to the age of node B (angiosperms), not the age of node A (angiosperms). The earliest Cretaceous forms are too rare and poorly known for definite statements, but at least from the Aptian onward, all angiosperm-like fossils described so far have angiosperm states in all of their available characters. None are clearly angiosperm-like in some characters but plesiomorphic (gymnosperm-like) in others, as would be expected of stem angiosperms. Of course, this might change with new discoveries (e.g., association of now-separate organs).

More definite dating of node B depends on

TABLE 1. Subdivisions of the Cretaceous.

Epoch/Series	Age/Stage
Late/Upper	Maastrichtian
	Campanian
	Santonian
	Coniacian
	Turonian
	Cenomanian
Early/Lower	Albian
	Aptian
	Barremian
	Hauterivian
	Valanginian
	Berriasian

recognition of separate lines leading to extant angiosperm subgroups. For this purpose, cladistic studies on modern angiosperms have been informative. In Donoghue and Doyle (1989), we analyzed relationships among basic lines of extant angiosperms using outgroups inferred from our seed plant analysis to polarize characters. Most of our shortest trees (e.g., fig. 9) show five major clades: Magnoliales at the base, Laurales, winteroids (Winteraceae, Illiciales), eudicots (the bulk of "dicots," with tricolpate and derived pollen, called "tricolpates" in Donoghue and Doyle 1989, but renamed by Doyle and Hotton 1991), and paleoherbs (herbaceous magnoliids and monocots). Eudicots are linked with paleoherbs based on characters such as palmate leaf venation. These results further strengthen the classical views on trends that were confirmed by the Cretaceous record: monosulcate pollen and simple leaves are basal, tricolpate pollen and compound leaves are restricted to the derived eudicot clade, and tricolporate and triporate pollen occurs in groups that are presumably nested higher within eudicots (Rosidae, Dilleniidae, Asteridae, and "Amentiferae" or "higher" Hamamelidae).

A major uncertainty concerns the position of the root of the tree. In our most parsimonious trees, the root is next to or among Magnoliales, but we also found trees only one or two steps longer that are rooted next to or among the paleoherbs. This "paleoherb rooting" deserves special attention because it is also seen in trees based on recent analyses of

ribosomal RNA (rRNA) sequences by Hamby and Zimmer (1992; fig. 10). In their trees, Nymphaeales (waterlilies) are basal, followed by Piperales, Aristolochiaceae plus monocots, and then a large clade including eudicots and woody magnoliids, within which relationships are poorly resolved. However, this uncertainty does not affect our estimate of the age of node B, or the conclusions just mentioned concerning trends.

These phylogenetic results can be integrated with the Cretaceous fossil record by using the distribution of characters on trees to determine the most likely position of fossils (Donoghue and Doyle 1989; Ward et al. 1989; Doyle et al. 1990a,b; Doyle and Hotton 1991; fig. 9). This exercise indicates that all five major clades were represented in the Barremian or early Aptian, before the main expansion of angiosperms (mostly tricolpate eudicots) in the Albian: Magnoliales by large, granular monosulcate pollen (*Lethomasites* Ward et al. 1989); Laurales close to Chloranthaceae by *Clavatipollenites* (confirmed by association with fossil fruits similar to but more primitive than those of extant Chloranthaceae: Pedersen et al. 1991) and possibly *Brenneripollis* and *Tucanopollis* (Walker and Walker 1984; Doyle and Hotton 1991); winteroids by ulcerate tetrads and possibly related zonasulculate pollen (*Walkeripollis*, *Afropollis*, *Schrankipollis*: Walker et al. 1983; Doyle et al. 1990a,b); eudicots by asymmetrical tricolpate pollen from Northern Gondwana (Brenner 1976; Doyle et al. 1977; Doyle and Hotton 1991); and paleoherbs by palmately veined leaves and monocot-like leaves and pollen (*Proteaephyllum reniforme*, *Acaciaephyllum*, *Liliacidites*, etc.: Doyle 1973; Doyle and Hickey 1976; Hickey and Doyle 1977; Walker and Walker 1984; Taylor and Hickey 1990). In the lower Potomac Group (Aptian) there are also leaves comparable to Magnoliales, Laurales, and winteroids but too generalized to be assigned to any one of these clades, with poorly organized pinnate venation and entire margins (*Ficophyllum*, *Rogersia*) or chloranthoid teeth (Wolfe et al. 1975; Doyle and Hickey 1976; Hickey and Doyle 1977; Upchurch 1984).

These results clearly indicate that some diversification of the crown-group had oc-

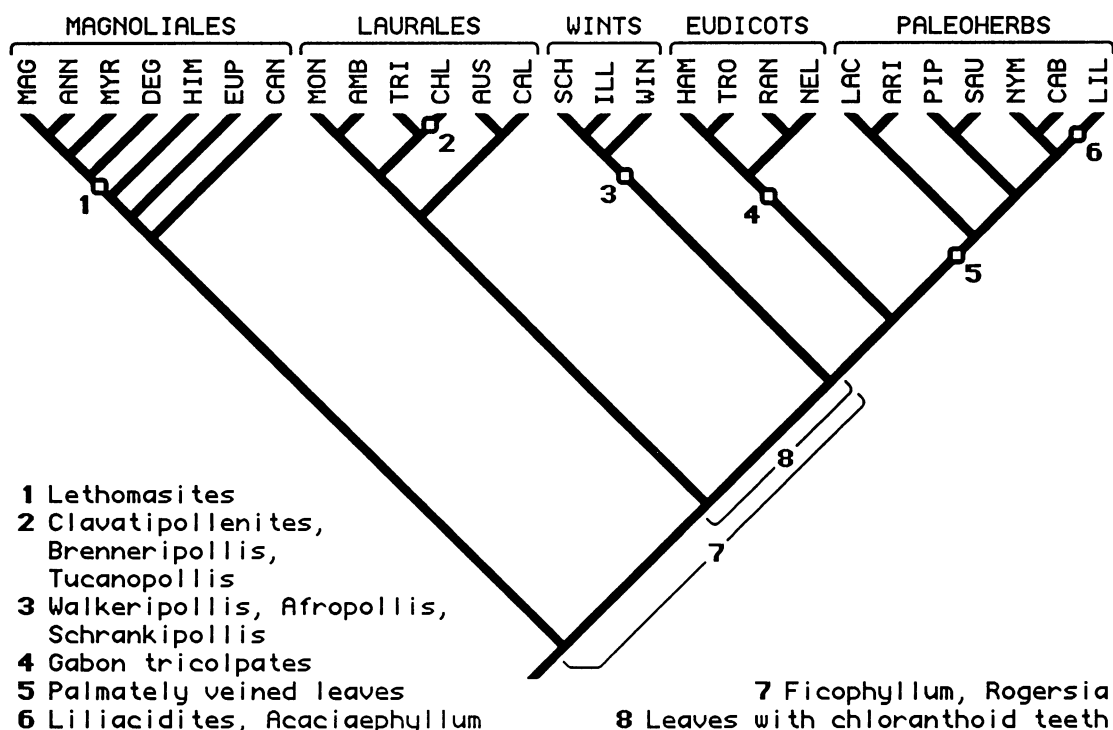


FIGURE 9. Representative most parsimonious angiosperm cladogram of Donoghue and Doyle (1989), with most likely positions of Barremian–Aptian fossils (1–8). MAG, Magnoliaceae; ANN, Annonaceae; MYR, Myristicaceae; DEG, Degeneriaceae; HIM, Himantandraceae; EUP, Eupomatiaceae; CAN, Canellaceae; MON, Monimiaceae *s. lat.*, Gomortegaceae, Hernandiaceae, Lauraceae; AMB, Amborellaceae; TRI, Trimeniaceae; CHL, Chloranthaceae; AUS, Austrobaileyaceae; CAL, Calycanthaceae; SCH, Schisandraceae; ILL, Illiciaceae; WIN, Winteraceae; HAM, Hamamelidales (and probably all “higher” eudicots); TRO, Trochodendrales; RAN, Ranunculidae; NEL, Nelumbonaceae; LAC, Lactoridaceae; ARI, Aristolochiaceae; PIP, Piperaceae; SAU, Saururaceae; NYM, Nymphaeaceae; CAB, Cabombaceae; LIL, monocots (Liliopsida); WINTS, winteroids.

curred before the Barremian. However, the inferred amount of diversification is far less than assumed by Axelrod (1952, 1970), who accepted identifications of taxa nested well within monocots (palms) and eudicots (Dipterocarpaceae, Icacinaceae) from before the Albian. Besides including representatives of the most basal lines of modern angiosperms, Barremian–Aptian fossils occupy a lower level of advancement than most modern members of these lines. Still, the discrepancy between the estimated Triassic and Early Cretaceous ages of nodes A and B might be taken as partial vindication of Axelrod’s view that angiosperms had a long pre-Cretaceous history. However, this discrepancy could have several other explanations. For example, it is possible that for most of this time the angiosperm line consisted of stem angiosphytes with few obvious angiosperm features. The large

number of apomorphies that accumulated on the stem-lineage (at least nine found only in angiosperms, plus three convergences with Gnetales or *Caytonia*: Doyle and Donoghue 1986) might support this scenario. Our trees imply that early angiosphytes would look like Bennettitales in most characters (leaf form, stomates, wood, pollen) with the exception of nodal anatomy and sporophyll morphology (Doyle and Donoghue 1986). Since the latter are rarely preserved, it is possible that pre-Cretaceous angiosphytes are already known but not recognized as such. Another possibility is that our cladogram is wrong, and node A is closer to the Cretaceous. The large gap in which no forms with the requisite character combinations are known represents a “stratigraphic parsimony debt” (Fisher 1980; Doyle et al. 1982) that could be regarded as evidence against our tree and in

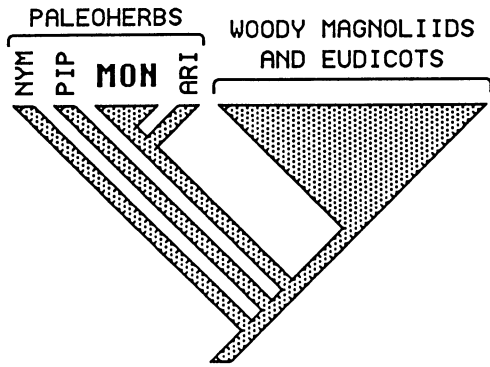


FIGURE 10. Simplified paleoherb-rooted angiosperm tree based on analysis of rRNA sequences (Hamby and Zimmer 1992). NYM, Nymphaeales (Nymphaeaceae plus Cabombaceae); PIP, Piperales (Piperaceae plus Saururaceae); MON, monocots; ARI, Aristolochiaceae.

favor of alternative trees in which angiosperms are nested within some group that we have assumed to be monophyletic, such as Bennettitales (as argued by Meyen 1988) or *Caytonia* (cf. fig. 6b). Such trees are only slightly less parsimonious in terms of our seed plant data set (Doyle and Donoghue 1986).

Another approach to dating nodes A and B combines trees with the assumption of a molecular clock. However, existing attempts omit the extant sister group of angiosperms, Gnetales, and thus provide no date for node A. Furthermore, they give highly inconsistent dates for node B. Martin et al. (1989), using DNA sequences of the glycolytic enzyme GAPDH, included no outgroups at all and calculated ages by assuming a rate of nucleotide substitution inferred from other eukaryotes. This placed the split into monocots and dicots in the Carboniferous and the split of dicots into *Magnolia* and several eudicots in the Permian. This estimate is grossly inconsistent with the fossil record, especially considering that eudicots are united by distinctive and readily preserved tricolpate or derived pollen, which does not appear until near the Barremian–Aptian boundary and becomes ubiquitous soon after (Crane et al. 1989). Wolfe et al. (1989), using DNA sequences of several chloroplast genes, included a liverwort (assumed to have split from vascular plants before the Devonian) and two green algae as outgroups. This gave the less extreme date of Early Jurassic for the eudicot–monocot

split (an estimate of node B), which is older than the Cretaceous evidence for the crown-group but does not contradict our Triassic estimate for node A.

Scenarios for Angiosperm Diversification

The following discussion, on causal interpretations of the angiosperm radiation and events leading up to it, focuses on several separate but intimately related questions. These have been perennial topics in angiosperm evolution, but cladistic analyses and new data put them in a significantly new light.

One issue is how specific features of angiosperms may have promoted their diversity and/or ecological success relative to other groups of plants. Here a key question is the sequence of origin of apomorphies that might promote diversity: whether they arose in the common ancestor of all angiosperms or in one or more subgroups within angiosperms (a question also posed by Crane and Lidgard 1990). This in turn places certain constraints on hypotheses concerning the origin of features that distinguish angiosperms from other groups.

A second question concerns the role of extrinsic vs. intrinsic factors in angiosperm diversification (cf. Cracraft 1982, or the environmentalist–internalist distinction of Gould 1977). In particular, we stress whether the radiation was triggered by changes in the physical or biotic environment (Cracraft 1982) or by origin of new features of the plants themselves, either key adaptations to existing but underexploited environments (Simpson 1953) or new features with incidental effects on speciation or extinction rates (Vrba 1983). Rate of diversification is of course a function of the interaction of both extrinsic and intrinsic factors, and it is artificial to separate the two, especially inasmuch as changes in organisms effectively create new environments (Lewontin 1983; Crane and Lidgard 1990). Nevertheless, it may be instructive to consider the relative timing of intrinsic and extrinsic events, especially whether a particular climatic or ecological setting existed or was widespread before or after the origin of particular features. This is not exactly the same as the previous question; the origin of attri-

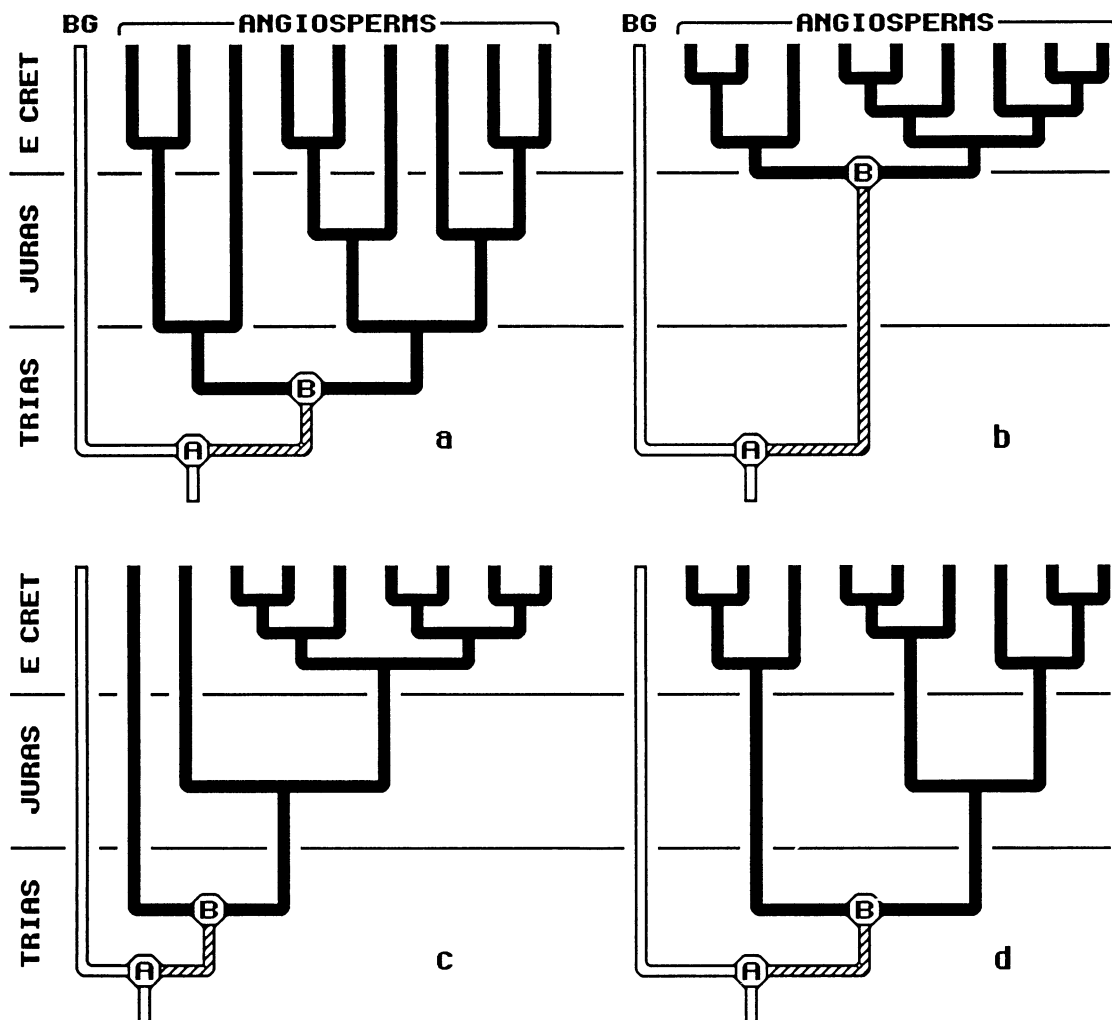


FIGURE 11. Four scenarios for the timing of angiosperm diversification. Scenario a corresponds to the view that angiosperms (the crown-group) originated and radiated extensively before the Cretaceous; b, that angiosperms originated not long before their observed radiation; c and d, that angiosperms originated in the Triassic but radiated in the Cretaceous, with magnolialian and paleoherb rootings, respectively. In c, pre-Cretaceous diversification might have been inhibited by intrinsic factors; in d, by extrinsic factors. BG, Bennettitales, *Pentoxylon*, and Gnetales.

butes favoring diversification may be a decisive intrinsic factor if the appropriate environmental conditions already exist, whereas in other cases such features may already have evolved but an external environmental change is required for diversification. In other words, the propensity of groups with particular intrinsic features to diversify may vary depending on extrinsic changes.

A final question concerns the pre-Cretaceous history of the angiosperm line. One view (cf. Axelrod 1952, 1970) is that angiosperms acquired the familiar apomorphies of

angiosperms and began splitting into extant lineages (node B) soon after splitting from their sister group (node A), and radiated actively through the Triassic and Jurassic (fig. 11a). At the other extreme is the view that angiosperms did not originate until the beginning of the Cretaceous and then radiated immediately; their Triassic and Jurassic precursors were stem angiosperms with some but not all of the apomorphies of extant forms (fig. 11b). The character of the Cretaceous record argues against the first view and is consistent with the second. However, it does not

rule out a third view (fig. 11c,d), i.e., that angiosperms split into a few primitive crown-group lines before the Cretaceous, but these have escaped detection because they had gymnosperm-like monosulcate pollen and did not diversify significantly until the Cretaceous (Doyle 1969; Muller 1970). A general challenge for such scenarios is to explain why angiosperms remained undiverse for so long when they radiated so vigorously in the Cretaceous (Doyle 1978). One possibility (fig. 11c) is that pre-Cretaceous angiosperms lacked some key intrinsic feature required for diversification. If this feature originated in one crown-group line, we would expect that descendants of this line would account for most of the diversity of extant angiosperms. Another possibility (fig. 11d) is that diversification was inhibited by extrinsic factors (e.g., herbivores, competitors, or unfavorable climates), or that it was stimulated by the appearance of new environments. An analogy would be the radiation of mammals, which remained undiverse until the extinction of dinosaurs at the end of the Cretaceous. If the pre-Cretaceous lines had the same intrinsic potential for diversification, more than one of them might have given rise to a large portion of extant angiosperms.

The Rooting Problem.—Probably the most significant issue raised by cladistic analyses of angiosperms concerns rooting of the angiosperm tree, which is uncertain because of the large number of characters that we were unable to polarize using outgroup comparison (Donoghue and Doyle 1989). Our shortest trees, where Magnoliales are the sister group of all other angiosperms (fig. 9) or a basal paraphyletic group, agree with the "classical" view that Magnoliales, Laurales, and winteroids, often called "woody magnoliids," represent a primitive grade of angiosperm evolution (e.g., Cronquist 1968, 1981; Takhtajan 1969, 1980; Thorne 1976). The recent analysis of Loconte and Stevenson (1991) also roots the angiosperms among woody magnoliids, but differs in placing Calycanthaceae and Idiospermaceae (combined in fig. 9) at the base; the difference is due in part to use of Recent outgroups only, a questionable procedure (Doyle and Donoghue 1987, 1992).

In contrast, our almost equally parsimonious trees with the root either next to or among the paleoherbs and the similar rRNA trees of Hamby and Zimmer (1992: fig. 10) imply that woody magnoliids are not a basal grade, but rather a derived clade (although they still are more primitive than most modern angiosperms). These trees give a very different picture of the first angiosperms (recalling views of Burger 1977, 1981a): they would be semi-herbaceous plants with palmately veined leaves, trimerous flowers, and stamens well differentiated into anther and filament, rather than woody plants with pinnately veined leaves, numerous spirally arranged floral parts, and laminar stamens. This ambiguity is not resolved by the Cretaceous record, which does not indicate whether woody magnoliids or paleoherbs are older. Experiments with Hamby and Zimmer's data set (J. A. Doyle, M. J. Donoghue, and E. A. Zimmer in preparation) indicate that although many details of their trees are weakly supported, the conclusion that paleoherbs are basal and Magnoliales are nested within angiosperms is highly robust. The strongest conclusion of these experiments is that both angiosperms and Gnetales are monophyletic groups, despite persistent claims to the contrary (Hughes 1976; Krassilov 1977, 1991; cf. Donoghue and Doyle 1991).

The view that paleoherbs are primitive has also been promoted by Taylor and Hickey (1990, 1992), stimulated by recognition of a paleoherb-like fossil with palmately veined leaves and an inflorescence of minute flowers from the Aptian of Australia and supported by a cladistic analysis. However, the similarity to other versions of the paleoherb hypothesis is only partial; Chloranthaceae and Piperales are the first two branches of Taylor and Hickey's tree, whereas our data and those of Hamby and Zimmer (1992) imply that Chloranthaceae do not belong near Piperales but rather among woody magnoliids. Their placement of Chloranthaceae and Piperaceae may be influenced by incomplete sampling of potentially related taxa and inclusion of several closely correlated ovule characters (relation of outer integument to funiculus, ovule angle, relation of funiculus to micro-

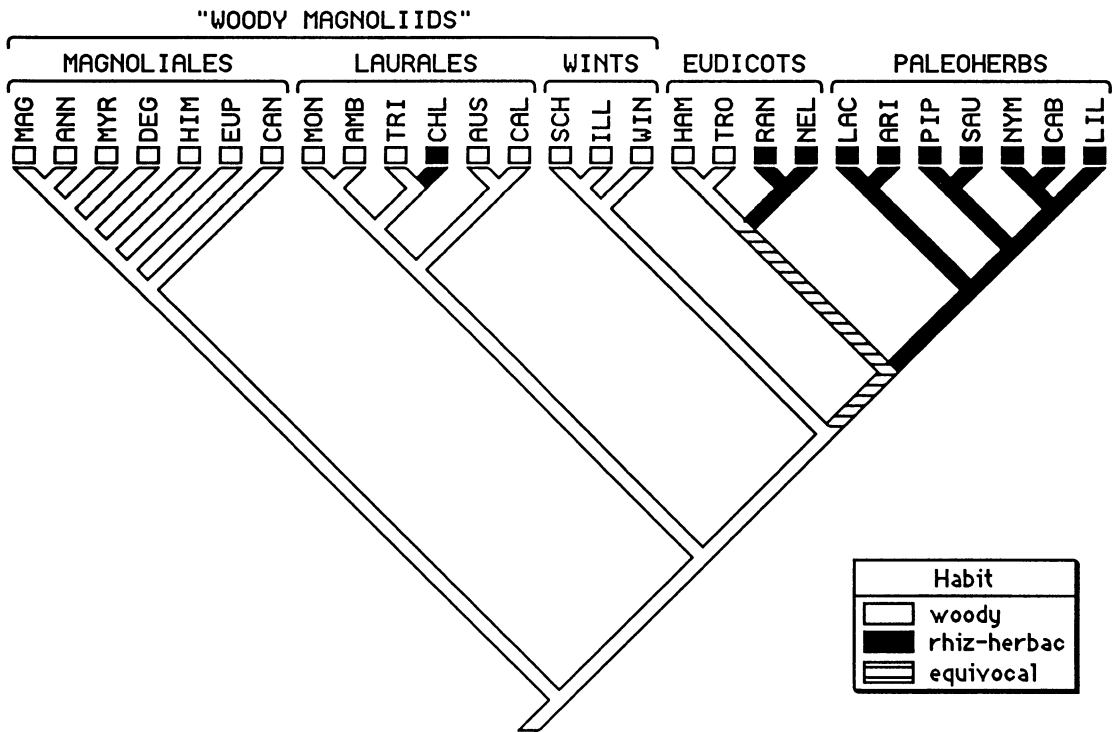


FIGURE 12. Magnolialian-rooted angiosperm tree (fig. 9), showing the distribution of woody vs. rhizomatous-herbaceous habit (a character not used in the original analysis).

pyle). In addition, their argument, based on presence of a paleoherb in the Aptian, is inconclusive since there is evidence that woody magnoliids existed at the same time.

Magnolialian Rooting.—If trees rooted near Magnoliales are correct (fig. 12), most angiosperm diversity resides in one major clade nested within the group. Nearly 98% of angiosperm species are paleoherbs or eudicots (all but about 5600 of 220,000 species: Cronquist 1981). In contrast, many woody magnoliid families consist of only one or two species (Eupomatiaceae, Himantandraceae, Degeneriaceae, Austrobaileyaceae, Idiospermaceae, Amborellaceae, Hortoniaceae, Gomortegaceae), and most of the remaining species belong to two families that are nested well within their respective orders (Annonaceae in Magnoliales, Lauraceae in Laurales). When making such comparisons, it is important to know whether the shift in diversification rate occurred at the base of the diverse clade or within it (cf. fig. 3), ideally combining information on phylogenetic trees with stratigraphic information on the timing

of diversification. To some extent, the higher diversity of paleoherbs and eudicots is a function of the existence of several extremely speciose groups nested well within the two clades, such as grasses, orchids, legumes, and composites, which radiated in the Tertiary (Muller 1981). However, this is not the whole explanation for the disparity because there are several diverse groups near the base of both lines, i.e., Piperales (2000 species) and Aristolochiaceae (600 species) in paleoherbs, and Ranunculales (3200 species) in eudicots. Furthermore, although the situation in paleoherbs is unclear because of their less diagnostic pollen, the record of tricolpate and derived pollen implies that eudicots began proliferating rapidly immediately after their appearance in the Barremian-Aptian.

One explanation for this disparity could be that woody magnoliids were once more diverse and were later decimated by extinction, but this does not seem to be the whole story. Although they did undergo significant attrition at the Cretaceous-Tertiary boundary (Upchurch 1989), they apparently radiated less

vigorously than other groups from the start. Woody magnoliids are known from the Barremian–Aptian, including the pollen types and lower Potomac Group leaves listed above. However, the leaves are rare and largely restricted to stream-margin facies (Doyle and Hickey 1976; Hickey and Doyle 1977; Crane 1987b). The pollen types are also rare, with the occasional exception of *Clavatipollenites*, *Brenneripollis*, and *Tucanopollis*, thought to be related to the laurialian family Chloranthaceae (Walker and Walker 1984; Doyle and Hotton 1991; Pedersen et al. 1991), and *Afropollis*, thought to be related to winteroids (Doyle et al. 1990a,b). The first abundant angiosperms, in the Albian, are eudicots (tricolpate pollen, *Sapindopsis* and platanoid leaves: Upchurch 1984; Friis and Crane 1989) or forms that could be either paleoherbs or eudicots (*Nelumbites*, cordate leaves). These still seem to prefer stream-margin facies but are locally dominant; there are few obvious woody magnoliids associated with them. There is more evidence of woody magnoliids in the Cenomanian, including lauraceous inflorescences (*Mauldinia*: Drinnan et al. 1990), flowers that may represent a stem relative of Magnoliaceae (*Archaeanthus*: Dilcher and Crane 1984), and leaves resembling higher Laurales and Magnoliales (Upchurch and Dilcher 1990). Interestingly, these seem to represent advanced members of their respective clades, potentially with diversity-enhancing attributes not shared with other woody magnoliids.

These considerations put a new perspective on discussions of angiosperm diversification, which have focused on explaining the diversity and/or ecological success of angiosperms relative to other groups of seed plants by asking how features shared by all angiosperms may have promoted their diversification. For example, our own previous discussions stressed the role of insect pollination in allowing dispersed distributions, thus promoting escape from herbivores and packing of more species into a given area (Doyle et al. 1982; cf. Janzen 1970; Burger 1981b), or the incidental effects of carpel closure in increasing the probability of reproductive isolation and speciation (Doyle and Donoghue 1986;

cf. Stanley 1979; Vrba 1983). However, if angiosperms are rooted near Magnoliales and most of their diversity is a consequence of the origin of the paleoherb–eudicot clade, attempts to explain the diversification should shift attention away from attributes arising at the base of the angiosperm tree and focus instead on synapomorphies of paleoherbs and eudicots.

As an example of this approach, we argued that the paleoherb–eudicot clade may have been originally more herbaceous than most modern hamamelids, and we suggested that this might explain its diversity (Donoghue and Doyle 1989: p. 36). This recalls the views of Stebbins (1974, 1981) and Bond (1989) that rapid and flexible growth was more important for angiosperm diversity and ecological success than insect pollination or animal dispersal. This shift was not obvious from our cladogram, because we distinguished woody and herbaceous based on presence or absence of a cambium, and we therefore plotted herbaceousness as arising in *Nelumbo* and the common ancestor of Piperales, Nymphaeales, and monocots. However, examination of the other taxa suggests that a shift to a “weedy,” rhizomatous, colonizing habit occurred at the base of the paleoherb–eudicot clade (fig. 12). In the paleoherbs, Aristolochiaceae are rhizomatous or viny plants with limited secondary wood of an anomalous type often attributed to secondary woodiness, and *Lactoris* is rhizomatous. In the eudicots, Ranunculidae range from anomalously woody to completely herbaceous. The other eudicot branch (including Trochodendrales, Hamamelidales, and probably all of the more advanced dicots) seems basically woody, but given the tree topology this woodiness is as likely to be secondarily derived as primitive. Furthermore, Albian members of this clade (palmately lobed platanoid leaves, pinnately compound *Sapindopsis*), though probably woody, have a stream-margin facies distribution and leaf morphology suggestive of fast-growing “weed trees” (Doyle and Hickey 1976; Hickey and Doyle 1977). We also noted that the most conspicuous exceptions to the early dominance of paleoherbs and eudicots are *Clavatipollenites* and similar forms, apparently re-

lated to Chloranthaceae, which are nested among woody Laurales but show a strong herbaceous tendency (Endress 1987).

If the initial diversification of angiosperms was connected with rapid growth and rhizomatous habit, it could be an example of a radiation triggered by intrinsic rather than extrinsic change (Doyle 1977). Angiosperms were the first major seed plant group with these features (Tiffney and Niklas 1985), with the possible exception of Gnetales (judging from the semi-herbaceous Potomac genus *Drewria* of Crane and Upchurch 1987 and the Brazilian Gnetales reported by Pons et al. 1992), which were radiating at the same time (Doyle et al. 1982; Crane and Lidgard 1989, 1990). These features may have promoted diversification by allowing radiation into disturbed habitats, which were presumably present but underexploited, or via a linkage between early reproduction and rapid diversification (Marzluff and Dial 1991). They may also have allowed invasion of aquatic habitats, occupied by Albian *Nelumbites* and possibly earlier monocots and reniforms (Doyle and Hickey 1976; Hickey and Doyle 1977). The principal earlier aquatic groups were Isoetales and Equisetales, spore-bearing plants of very different aspect. Extrinsic factors were apparently dominant in the late Tertiary radiation of advanced herbaceous angiosperms (e.g., grasses, Umbelliferae, Compositae), which coincides with global cooling and increase in seasonality, but there is no evidence for such a change in the Early Cretaceous. If anything, climates were becoming warmer, more moderate, and wetter, with an increase in rainfall in Southern Laurasia and the first appearance of an equatorial wet belt since the Carboniferous (Vakhrameev 1970; Doyle et al. 1982; Parrish et al. 1982; Parrish 1987). This does not rule out the importance of other extrinsic factors, including those discussed in the section on paleoherb-rooted trees.

This interpretation would contradict a scenario for the origin of angiosperms proposed by Doyle and Hickey (1976) and Doyle (1978), who argued that the first angiosperms were weedy forms and linked this weediness with their origin from a seed fern ancestor by progenesis. These ideas were based on the facies

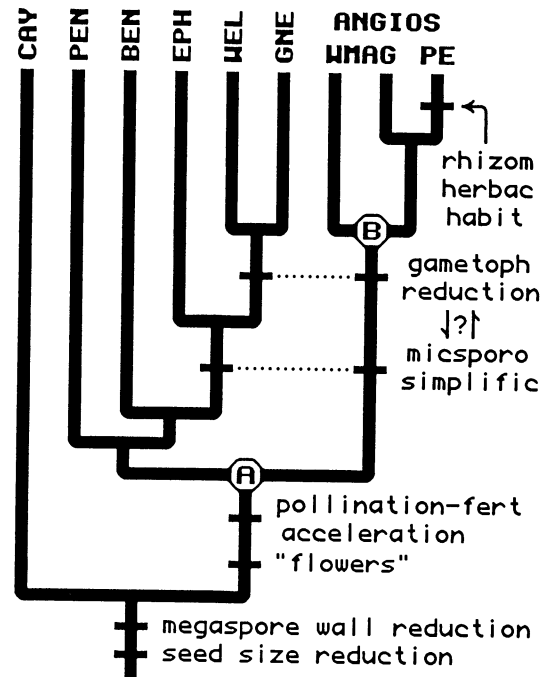


FIGURE 13. Stepwise origin of supposed progenetic features of angiosperms. Abbreviations of taxa as in figure 7; WMAG, "woody magnoliids"; PE, paleoherb-eudicot clade; rhizom herbac, rhizomatous-herbaceous; gametoph, gametophyte; microporo simplif, microsporophyll simplification; fert, fertilization.

distribution and morphology of Potomac Group leaves and the suggestion of Stebbins (1974) that many of the differences between angiosperms and other seed plants reflect a speed-up of the life cycle connected with adaptation to disturbed habitats (i.e., *r*-strategy). In contrast, trees rooted near Magnoliales imply that angiosperms were originally woody, and although a shift to weediness might be responsible for the Cretaceous radiation, this factor would apply only to the paleoherb-eudicot clade, not to angiosperms as a whole. In addition, examination of our seed plant trees (Doyle and Donoghue 1986, 1992) implies that the supposedly progenetic features of angiosperms originated at various points from below node A to above node B (fig. 13). Reduction of seed size and the megaspore wall presumably date back at least to the common ancestor of angiosperms and *Caytonia*. Aggregation of sporophylls into flowers and reduction of the time between pollination and fertilization presumably arose in the common

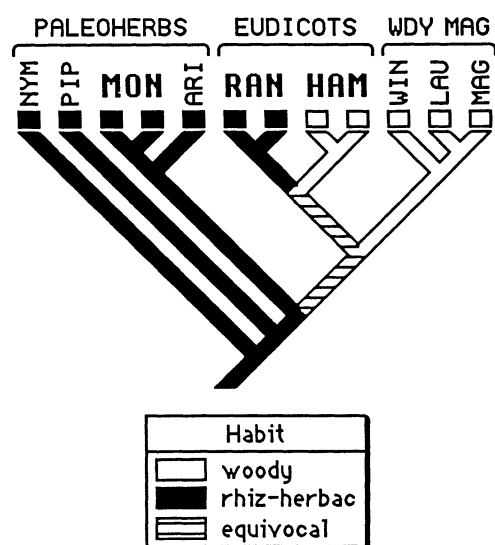


FIGURE 14. Paleoherb-rooted angiosperm tree (fig. 11), modified to incorporate relationships within the woody magnoliid-eudicot clade inferred from morphological analyses (fig. 9), showing the distribution of woody vs. rhizomatous-herbaceous habit. NYM, Nymphaeales; PIP, Piperales; MON, monocots; ARI, Aristolochiaceae; RAN, Ranunculidae; HAM, Hamamelidae and "higher" eudicots; WIN, winteroids; LAU, Laurales; MAG, Magnoliales.

ancestor of all anthophytes (node A). Simplification of the microsporophylls and gametophyte reduction (more extreme in angiosperms) occurred independently between nodes A and B and in Gnetales (in Gnetales, the tree specifies that microsporophylls were simplified first, but in angiosperms the order of changes is undefined). These observations also help us to tease apart which of the progenetic factors may have affected diversification rate; thus, seed reduction and gametophyte reduction may have had less effect than origin of flowers (shared with the fairly diverse Bennettiales) and change in habit.

Trees rooted near Magnoliales may be consistent with a scenario of the type in figure 11c, where angiosperms of a woody magnoliid type existed before the Cretaceous but did not radiate until the origin of the paleoherb-eudicot clade. Woody magnoliids today show a preference for habitats where they might escape preservation, namely wet, equable, upland tropical areas (Axelrod 1952; Takhtajan 1969; Carlquist 1975). Even if their pollen was washed into lowland basins, it might

be overlooked since it would be monosulcate with gymnosperm-like granular structure until the node below Laurales, where more diagnostic columellar structure arises, and even then it would be monosulcate and finely sculptured. As an argument against this concept, it is hard to believe that woody magnoliids would have remained so undiverse and ecologically restricted that none of them would be recognized. After all, there are some 5600 species of these plants today, which is not many compared with other angiosperms but is a large number compared with other seed plants (ca. 800 species today). It should be noted, however, that most of this diversity is in Annonaceae and Lauraceae, which are the exception to the rule in being concentrated in lowland rainforests. This environment may have been rare before the Cretaceous because of monsoonal circulation across the tropical belt (Parrish et al. 1982; Parrish 1987), and it may have remained relatively restricted until the Early Tertiary, when the first evidence of multistratal rainforest is seen at middle latitudes (Wolfe and Upchurch 1987).

Paleoherb Rooting.—Whereas trees rooted near Magnoliales imply that most of the diversity of angiosperms can be linked with the origin of one diverse clade within the group, this is not so with trees rooted among paleoherbs (Hamby and Zimmer 1992; fig. 14). Here the root is not attached among groups of low diversity, but rather among the most diverse early lines of angiosperms. Whatever attributes were responsible for the diversity of paleoherbs and eudicots might therefore be basic features of angiosperms as a whole, present since node B, and not later advances that arose within the group. This would be true of rhizomatous habit and colonizing abilities. These trees would also be more consistent with the hypothesis that many of the "progenetic" features of the angiosperm life cycle arose during a shift from slow-growing and woody to fast-growing and rhizomatous below node B (Stebbins 1974; Doyle and Hickey 1976; Doyle 1978).

An apparent contradiction to this scenario is the fact that the basal group in the rRNA trees is Nymphaeales, which consist of only

about 60 species (Cronquist 1981). This might be taken as evidence that angiosperms spent an initial phase in aquatic habitats where they diversified slowly and only later diversified rapidly as a result of reinvading the land. The highly reduced aquatic genus *Ceratophyllum*, considered an ancient lineage by Dilcher (1989) and Les et al. (1991), could be another derivative of an original aquatic phase. A more orthodox alternative is that the aquatic habit of Nymphaeales is an autapomorphy that inhibited their diversification because of its limited ecological potential.

In the context of paleoherb-rooted trees, the lower diversity of woody magnoliids takes on a different significance; the question is no longer why diversification sped up in paleoherbs and eudicots, but rather why it slowed down in woody magnoliids. The most obvious change in the critical region of the tree is a shift to woody habit. Paleoherb-rooted trees are more compatible with the view of Stebbins (1974) that the slow-growing, woody habit of most Magnoliales, Laurales, and winteroids originated as a result of a shift from disturbed habitats to stable forest environments, where rapid reproduction was no longer at a premium (i.e., *K*-strategy). Woody magnoliids may have been among the most common angiosperms in stable habitats after the initial expansion of angiosperms, as suggested by the Cenomanian Dakota flora described by Upchurch and Dilcher (1990), which differs from the classic stream-margin Dakota flora in representing a brackish-water swamp forest.

The view that a shift to forest environments contributed to the low relative diversity of woody magnoliids may seem to conflict with the fact that woody angiosperms in general are so diverse in modern rainforests, suggesting that speciation rates are unusually high in such habitats. However, this diversity may be a function of low extinction rates rather than high speciation rates (cf. Cracraft 1982); Stebbins (1974) argued that speciation is more common in marginal environments than in the forests themselves. Furthermore, climates suitable for multistratal rainforests may not have become widespread until the Early Tertiary (Wolfe and Upchurch 1987), by

which time there was a large number of eudicot lines that could take advantage of the same new environments. Finally, the diversity of modern rainforests may be in part a function of the Tertiary radiation of animal pollinators and dispersers (cf. Janzen 1970; Regal 1977; Burger 1981b; Wing and Tiffney 1987).

The paleoherb rooting also affects the plausibility of scenarios involving pre-Cretaceous angiosperms (i.e., members of the crown-group). It is less reasonable to postulate that such plants have not been detected because they were restricted to tropical uplands, since paleoherbs do not show the preference for such habitats as do woody magnoliids. Nymphaeales, being aquatic, show the opposite tendency, and primitive eudicots are most diverse in temperate areas. On the other hand, the well-known bias against fossilization of herbaceous plants might allow paleoherbs to exist before the Cretaceous without being seen (cf. Taylor and Hickey 1990). This would be more likely if they were terrestrial herbs rather than aquatics like Nymphaeales, which often grow in great numbers in environments of deposition and are commonly found as fossils in the Late Cretaceous and Tertiary. If paleoherb-like angiosperms remained undiverse, it is also conceivable that their pollen would escape recognition. Many paleoherbs have more distinctive pollen than most Magnoliales (e.g., prominently sculptured monocots), but the basal groups have almost equally gymnosperm-like pollen (large in Nymphaeales, small in Piperales, but in both cases monosulcate with nearly invisible infratectal structure).

As with the magnolialian rooting, intrinsic paleoherb features such as rhizomatous habit and colonizing ability could play an important role in the radiation of angiosperms. However, these features would be present since the origin of angiosperms, not later advances of one clade. If angiosperms did not evolve until the Cretaceous (fig. 11b), it would be reasonable to suggest that origin of these features was what triggered their radiation, since disturbed habitats that such plants could exploit were presumably always present. Scenarios involving pre-Cretaceous angiosperms

would be of the sort where each of several existing lines (the ancestors of paleoherbs and eudicots) diversified in the Cretaceous (fig. 11d). This would seem to require either the simultaneous acquisition of diversity-enhancing features in each line, or (more likely) the existence of some extrinsic factor that inhibited angiosperm diversification in the Jurassic or stimulated it in the Cretaceous.

One extrinsic factor that might be linked to the angiosperm radiation is climatic equability. Defining equability in terms of low seasonality and moderate temperatures, Axelrod (1970) argued that the only equable areas in the Jurassic were the tropical uplands (low-latitude lowlands were too hot and arid, high-latitude areas too seasonal) and he attributed the Cretaceous spread of angiosperms to a global increase in equability due to continental fragmentation. However, although this scenario might make sense if early angiosperms were like woody magnoliids, it does not if they were like paleoherbs. Furthermore, it is debatable that there were no equable lowlands in the Jurassic; certainly the Yorkshire Middle Jurassic flora looks mesic and predominantly evergreen but was not far from the boundary of the temperate Siberian flora, which is known from Scotland in the Late Jurassic (Vakhrameev 1970). Finally, Axelrod's scenario conflicts with the fact that angiosperms appeared as early in arid tropical lowlands as in the presumably more equable middle latitudes, or earlier (Brenner 1976; Doyle et al. 1977, 1982; Brenner and Crepet 1986; Trevisan 1988), and some of them reached high southern latitudes by the Aptian (Taylor and Hickey 1990).

Although there were no extrinsic changes as obvious as Tertiary cooling that might have caused a delayed radiation of paleoherb-like angiosperms, more subtle environmental trends were occurring near the Jurassic-Cretaceous transition. Except for an arid phase in the Late Jurassic of Southern Laurasia, Jurassic environments and floras were remarkably uniform and stable, apparently due to unusually low tectonic activity, relief, and climatic gradients (Vakhrameev 1970; Hallam 1975). In contrast, tectonic activity resumed in the Early Cretaceous (e.g., rifting of the

South Atlantic), and environments of continental deposition subject to constant fluvial disturbance increased in area due to rifting and sea level rise (e.g., Potomac, Wealden, Kazakhstan, and Cocobeach sequences). There are no obvious extinctions of competitors that might have played a role analogous to the extinction of dinosaurs for mammals. However, Bakker (1978) argued that increasing herbivore disturbance due to a change in the dinosaur fauna, from predominantly high-browsing in the Jurassic to low-browsing in the Early Cretaceous, may have favored fast-growing angiosperms over other seed plants and stimulated their diversification. Although local disturbed habitats that paleoherbs could exploit presumably always existed, these global increases in environmental heterogeneity and instability may have provided a critical stimulus to their radiation.

These trends might have affected diversification of angiosperms whether or not they were like paleoherbs; in fact, angiosperms may be part of a more general pattern. Cracraft (1982) argued that speciation rate is controlled primarily by "lithospheric complexity, which relates directly to the number of geological and climatic barriers promoting geographic isolation." In general, the plant fossil record shows a pattern of proliferation of new groups in the Late Triassic (also a time of tectonic activity), stagnation in the Jurassic, and renewed diversification in the Early Cretaceous. The histograms of Niklas et al. (1980) show a Jurassic minimum in species diversity (although this may be biased by emphasis on data from North America, where Jurassic floras are rare and poorly studied). With a few exceptions (Dicksoniaceae, early Schizaeaceae, Araucariaceae), most Jurassic plant groups had appeared in the Triassic, but in the latest Jurassic and Early Cretaceous there was a conspicuous diversification of Schizaeaceae (with striate and verrucate spores), Pinaceae, Taxodiaceae, Cheirolepidiaceae (*Frenelopsis* and related forms), Bennettitales (*Cycadeoidea*), and Gnetales (ephedroid pollen). A mass extinction at the Triassic-Jurassic boundary (Tucker and Benton 1982; Olsen et al. 1987) may have contributed to this pattern by truncating many

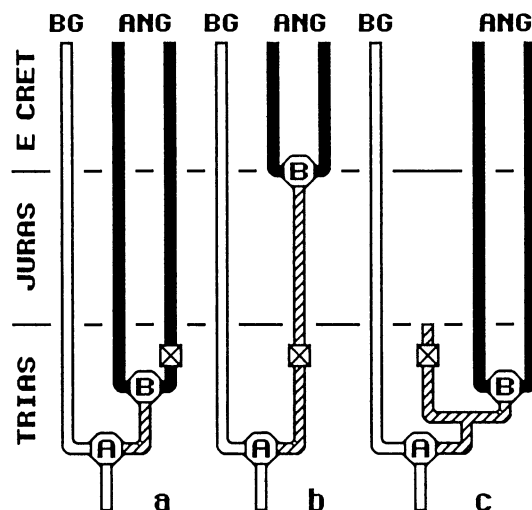
new lines, but other factors such as environmental uniformity are needed to explain why diversity did not rebound in the Jurassic. Other changes that may have stimulated plant diversification in the Early Cretaceous were an increase in rainfall in Southern Laurasia, attributed to widening of the central Atlantic, and origin of an equatorial wet belt, attributed to the breakdown of monsoonal circulation (Vakhrameev 1970; Parrish et al. 1982; Parrish 1987).

These extrinsic factors might not be sufficient individually, but together they might have kept the crown-group limited to a few slowly diversifying, ecologically restricted lines during the Jurassic, which then radiated in the Early Cretaceous (fig. 11d). The same factors might also have kept the angiosperm line rare and undiverse in the Jurassic if it consisted entirely of stem angiosperms (fig. 11b). Either way, angiosperms would have "gone into a tunnel" in the Jurassic. The plausibility of this view is enhanced by the fact that the related Gnetales seem to have had an analogous history: ephedroid pollen is known in the Late Triassic (when it probably represents stem relatives of Gnetales: see above), disappears almost completely in the Jurassic, but then proliferates in the Early Cretaceous, in the same tropical areas where angiosperms were most abundant. It is also noteworthy that Early Cretaceous Gnetales included semi-herbaceous forms and apparently preferred the same fluvial facies as early angiosperms (Doyle et al. 1982; Crane and Upchurch 1987; Crane and Lidgard 1989, 1990; Pons et al. 1992).

Implications of Pre-Cretaceous Fossils

The alternatives we have outlined would be easier to evaluate if we had direct evidence on the status of the angiosperm line before the Cretaceous. Better information on the diversity of other anthophytes might also help; most of our knowledge is based on a few specialized taxa, and it is possible that other less well-known forms have character combinations that would modify ideas on basic states in outgroups and therefore in angiosperms themselves.

There is no lack of supposed pre-Creta-



☒ Late Triassic fossil

FIGURE 15. Implications of Late Triassic angiosperm-like fossils (*Sanmiguelia*, *Crinopolles*) for the age of node B, depending on whether they are angiosperms (a) or stem angiosperms; in the latter case, the crown-group could be much younger (b), or it could exist at the same time (c). BG, Bennettitales, *Pentoxylon*, and Gnetales.

ceous angiosperms (Axelrod 1952, 1970), but most have been shown to be unrelated to angiosperms, incorrectly dated, or possibly related to angiosperms but lacking sufficient diagnostic characters for interpretation (Scott et al. 1960; Hughes 1961, 1976; Hickey and Doyle 1977; Doyle 1978). However, there have been several promising recent discoveries and new insights on older ones. Again, our point is that consideration of how such fossils fit into phylogenetic trees is of prime importance in evaluating their significance. A critical question in each case is whether the fossil has angiosperm states in all its known characters, making it a potential member of the crown-group, or a mixture of angiosperm advances and more plesiomorphic states, placing it along the stem-lineage. Depending on how completely they were known, fossils of the first sort would constitute evidence that node B had been reached (fig. 15a). Fossils of the second sort might mean that the crown-group had not yet originated (fig. 15b), although it could not be excluded that the crown-group existed at the same time but has not been detected (fig. 15c). Unfortunately, none of the fossils in question fall unequiv-

ocally in either category. However, the best candidates are all suggestive in showing states more like paleoherbs than woody magnoliids. If they are angiosperms, they could mean either that paleoherbs are primitive, or that angiosperms had split into paleoherbs and woody magnoliids but the latter have not yet been found; if they are stem angiosperms, they would definitely favor the view that paleoherb features are primitive in angiosperms.

The best-known putative pre-Cretaceous angiosperm is *Sanmiguelia*, first described from the Upper Triassic of Colorado as a palm-like pleated leaf (Brown 1956) but questioned because it lacks the diagnostic midrib of palms (Read and Hickey 1972) and was too poorly preserved to show whether it had the finer cross-veins diagnostic of monocots (Doyle 1973). This situation has changed with Cornet's (1986, 1989b) discovery of better material from the Upper Triassic of Texas, including both leaves and putatively connected stems and reproductive structures. However, the status of *Sanmiguelia* still remains problematic (cf. Crane 1987a). The leaves do show cross-veins, although in some cases these may be artifacts of shredding. The stems have secondary wood, unlike monocots, but of a primitive vessel-less type, as in most "gymnosperms" and a few dicots; this implies that *Sanmiguelia* does not belong within the monocots, but it could be a stem relative of that group. The male structures are the least angiosperm-like: they consist of secondary axes bearing numerous sessile pairs of pollen sacs, unlike angiosperm stamens with two lateral pairs of sacs. Although Cornet (1989b) argued that these structures could be transformed into an angiosperm stamen, they are more readily compared with ginkgophyte strobili bearing sporophylls with two pollen sacs. The pollen is of a glassy, monosulcate type that Cornet compared with granular Magnoliales, but it is equally comparable with Bennettitales or Ginkgoales. Potentially most diagnostic are the female structures, interpreted as flowers with a perianth and carpels containing anatropous ovules, but we are not convinced that the preservation is clear enough to warrant Cornet's detailed reconstruction. The best alternative relationships may be with the gink-

gophyte order Czekanowskiales or with Gnetales (a stem relative before origin of opposite leaves, vessels, and striate pollen); both have parallel-veined leaves that could be modified into the *Sanmiguelia* type.

If *Sanmiguelia* turns out to be an angiosperm, the male structures suggest that it is attached to the angiosperm stem-lineage. If so, the monocot-like leaf morphology would favor rooting the angiosperm tree among paleoherbs rather than woody magnoliids. Conversely, if paleoherbs are basal in angiosperms, the pollen argues against assignment of *Sanmiguelia* to the crown-group, since paleoherbs seem basically columellar. Nymphaeales have been called granular, but Osborn et al. (1991) have shown that Cabombaceae actually have fine columellae, and the other family, Nymphaeaceae, needs reinvestigation.

Equally intriguing are several Late Triassic pollen genera described by Cornet (1989a) as the Crinopolles group (one also studied with scanning and transmission electron microscopy by Doyle and Hotton 1991). These are monosulcate (sometimes with lateral subsidiary furrows) and have strikingly angiosperm-like reticulate sculpture and well-developed columellae. The sculpture is unusual in grading from fine at the distal pole to coarse proximally. Graded sculpture also occurs in monocots (including Cretaceous *Liliacidites*: Doyle 1973), tricolpate eudicots (Trochodendrales, Cretaceous *Rousea*), and the Cretaceous monosulcate genus *Similipollis* (placed in *Liliacidites* by Doyle 1973 and Walker and Walker 1984), but the pattern of gradation is different (fine at the ends of the grain in monocots, fine at both poles in *Similipollis* and tricolpates). Cornet argued that Crinopolles are also angiosperm-like because the darker-staining endexine layer lacks the laminations characteristic of "gymnosperms." However, Doyle and Hotton (1991) pointed out that laminations are often not preserved in fossil pollen, and that Crinopolles are more plesiomorphic than modern angiosperms in having a thick endexine, like other seed plants, whereas in monosulcate angiosperms endexine is either lacking or largely restricted to below the sulcus. This suggests that Crino-

polles are either unrelated to angiosperms but convergent with them in having columellae and reticulate sculpture, or stem angiophytes. In the latter case, they might support trees rooted among paleoherbs and eudicots, since these are the extant groups where graded sculpture is found. It may be noted that this interpretation would conflict with the view that *Sanmiguelia* is a crown-group member, since it has more plesiomorphic unsculptured pollen with no sign of paleoherb features.

A final potentially relevant fossil is a single leaf described from the Middle Jurassic of England by Seward (1904) as *Phyllites*. This leaf resembles paleoherbs and primitive eudicots in having palmate-acrodromous venation; it is more paleoherb-like in having entire margins, whereas many (though not all) primitive eudicots have chloranthoid marginal teeth. If *Phyllites* is a stem angio-phyte, or an angiosperm that was representative of the whole crown-group at the time, it would again support a paleoherb rooting. However, in the absence of other organs or characters (e.g., no higher-order venation is preserved), it is impossible to decide between these alternatives, or even to rule out the possibility that it is a convergent non-angio-phyte.

Conclusions

We hope that our discussion of angiosperms has shown how phylogenetic trees can clarify and constrain scenarios for diversification. Although comparisons of fossils with trees based on extant angiosperms confirm that primitive angiosperms (the crown-group) radiated rapidly in the Early Cretaceous, analyses of seed plants as a whole imply that angiophytes (the angiosperm line) had originated by the Late Triassic. Phylogenetic analyses focus attention on rooting of the angiosperm tree as the most significant issue in understanding early angiosperm diversification. Trees rooted near Magnoliales suggest that the Cretaceous radiation was triggered by the evolution of intrinsic advances, such as the rhizomatous, "weedy" habit, in one line within angiosperms, which gave rise to the highly diverse paleoherbs and eudicots. In contrast, trees rooted among paleoherbs,

which are favored by rRNA data, suggest that traits linked to rapid radiation were basic for angiosperms as a whole. Such trees might favor the view that angiosperms originated not long before the Cretaceous. If it is found that they did originate earlier, it will be necessary to seek extrinsic factors that might have delayed their radiation, such as a general shift from uniform and stable conditions in the Jurassic to greater environmental heterogeneity and disturbance in the Early Cretaceous.

The significance of pre-Cretaceous fossils also depends on how they fit into phylogenetic trees. The Late Triassic fossils that are most likely related to angiosperms seem consistent with the view that the crown-group had not yet originated. If so, the fact that these fossils have paleoherb-like features would favor the paleoherb rooting. The failure of angiophytes to radiate might then be due to lack of intrinsic advances; perhaps they did not yet have some feature of extant paleoherbs, such as rapid growth rate, or perhaps they lacked some other basic angiosperm feature that was a prerequisite for radiation, such as closed carpels or accelerated reproduction. However, their delayed radiation could also be due in part to the extrinsic factors cited above.

In discussing so many alternatives, we may have given the impression that tree-thinking is more useful in generating hypotheses than in deciding among them. However, this would be unduly pessimistic. It is suggestive that both the rRNA evidence and pre-Cretaceous fossils point toward a paleoherb rooting and the scenarios it entails. We are also impressed by the parallels between the record of angiosperms and that of the related Gnetales when viewed from a phylogenetic and stratigraphic perspective (Doyle et al. 1982; Doyle and Donoghue 1986; Crane and Lidgard 1989, 1990). The first fossils comparable to Gnetales, also found in the Late Triassic (ephedroid pollen, *Dechellyia*, *Schilderia*), lack major advances of modern Gnetales and are probably stem relatives. Van Konijnenburg-van Cittert (1992) also isolated ephedroid pollen from Early Jurassic fossils with linear leaves and axillary reproductive structures that differ from those of modern Gne-

tales in having numerous ovules and microsyngamia. The gnetalian line almost disappeared in the Jurassic but radiated in the Early Cretaceous. As with angiosperms, this radiation apparently involved crown-group forms (*Eoantha*, *Drewria*, etc.). The ecological convergences between the two groups (accelerated life cycle, tendency to herbaceous habit, preference for disturbed, semiarid, tropical habitats) suggest that they may have responded in similar ways to extrinsic trends. Perhaps the two lines had parallel pre-Cretaceous histories: a "false start" in the Late Triassic, truncated by an extinction event and conditions uncondusive to diversification, then origin of the crown-group later in the Jurassic, associated with resumed climatic and tectonic changes at that time. This scenario would be intermediate between b and d in figure 11. In the Late Cretaceous, angiosperms continued their rise but Gnetales went into decline; reasons for this replacement, such as higher potential speciation rate in angiosperms and/or competitive superiority of new angiosperm clades, have been discussed by Doyle and Donoghue (1986) and Crane and Lidgard (1990).

These hypotheses could be further constrained by better information on other organs and characters of pre-Cretaceous fossils and/or a more confident placement of the root of the angiosperm tree based on additional molecular data. Finally, better understanding of Jurassic environments and the ecology of Mesozoic anthophyte groups could help constrain scenarios from the paleoecological side.

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