

THE IMPORTANCE OF FOSSILS IN ELUCIDATING SEED PLANT PHYLOGENY AND MACROEVOLUTION

JAMES A. DOYLE and MICHAEL J. DONOGHUE

Department of Botany, University of California, Davis, CA 95616 (U.S.A.)

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721 (U.S.A.)

(Revised and accepted August 19, 1986)

Abstract

Doyle, J.A. and Donoghue, M.J., 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Rev. Palaeobot. Palynol.*, 50: 63–95.

In order to gain insights on the controversial question of the value of fossils in understanding phylogeny and macroevolution, we used numerical parsimony methods to analyze a data set amassed for a cladistic study of living and fossil seed plants, variously modified by subtraction and re-addition of fossil groups. Some cladograms based on extant groups alone are consistent with relationships derived from the whole data set, but the direction of leaf and sporophyll evolution in seed plants and floral evolution in angiosperms and Gnetales is equivocal. However, use of Carboniferous seed ferns as outgroups favors the concept that all seed plants were derived from ancestors with fern-like leaves, that there was a double trend to linear-dichotomous leaves in coniferopsids and Gnetales, and that gnetalian flowers are reduced relative to those of angiosperms and Bennettitales, as inferred from the whole data set. With the whole data set, it is slightly more parsimonious to assume that coniferopsids were derived from *Callistophyton*-like platyspermic seed ferns than from *Archaeopteris*-like progymnosperms, but if *Archaeopteris* were unknown the seed fern hypothesis would be strongly favored, while if *Callistophyton* were unknown both hypotheses would be equally parsimonious. Bennettitales strengthen relationships between Gnetales and angiosperms, which are only slightly stronger than links between Gnetales and coniferopsids when extant data alone are considered, while *Caytonia* clarifies reproductive homologies of angiosperms, Bennettitales, and Gnetales and their origin from platyspermic ancestors. Although fossil information does not radically alter inferred relationships among extant taxa in seed plants, it may in other groups, and it provides unique evidence on the sequence of events and possible adaptive factors involved in the origin of groups. Both contributions are especially important when there has been extensive homoplasy and/or when living groups are isolated from each other by large gaps, as is often true of higher taxa.

Introduction

The role of fossil evidence in elucidating the relationships of major groups and evolutionary processes involved in their origin has recently become the subject of much debate, closely tied with the general revival of interest in phylogeny stimulated by cladistics, or phylogenetic systematics (Hennig, 1966). Whereas many paleontologists have considered fossils the best or even the only valid source of evidence on

relationships (Simpson, 1961; Hughes, 1976; Gingerich, 1979), cladists have assigned them a more limited role. Cladistic analysis provides a set of logical principles for formulating and testing phylogenetic hypotheses whether or not fossils are available: using shared derived traits (synapomorphies) as evidence of common ancestry, and most commonly determining polarities (ancestral and derived character states) by outgroup comparison and deciding among alternative hypotheses on the basis of parsimony.

mony (preferring the scheme that requires the fewest character state changes). Hennig (1966) argued that fossils provide phylogenetic information only in conjunction with comparative analysis of all characters, and as such they have many disadvantages relative to living organisms because of their incompleteness, making their detailed relationships difficult to determine (Hennig, 1966, pp.140–142). At the same time, he granted that fossils can be of great importance in the area of character analysis, which forms the basis of cladistic analysis of both living and fossil groups, and for this reason he urged closer study of those characters that are preserved in fossils (Hennig, 1966, pp.142, 165). He also accepted the stratigraphic order of appearance of character states as one source of evidence on polarity (Hennig, 1966, p.95). He noted that fossils are often valuable in filling the gaps in transformation series and revealing the sequence of acquisition of derived features, which may be decisive in determining the relationships of highly derived living groups and in showing that features that might be assumed to be homologous actually evolved independently within separate clades (Hennig, 1966, pp.142–145).

More recent discussions have explored the issues raised by Hennig to varying degrees, giving some points ample attention but largely neglecting others. For example, some authors (Nelson, 1978; Stevens, 1980) have criticized the use of stratigraphic evidence in polarity assessment, based in part on the fact that more advanced members of a group may appear before more primitive ones because of the incompleteness of the fossil record. However, more recently Eldredge and Novacek (1985) have argued that stratigraphy as well as outgroup comparison and ontogeny can provide valid evidence on polarity when the record of a group meets independently testable criteria of completeness. Others have suggested that the degree of agreement between the order of appearance of character combinations predicted by phylogenetic hypotheses and the stratigraphic record can be used as an independent basis for favoring some hypotheses over

others (Fisher, 1980; Doyle et al., 1982). Paleontologists have also come under much criticism for thinking in terms of ancestor–descendant relationships: “ancestral groups” are paraphyletic (incomplete) and therefore rejected by cladists as artificial, and even if rephrased in terms of species, ancestor–descendant relationships are thought to be less readily testable than sister-group relationships (Engelmann and Wiley, 1977; Platnick, 1977; Eldredge, 1979). Patterson (1981) argues that because of their emphasis on ancestors paleontologists have more often hindered understanding of phylogenetic relationships than advanced them. However, even if paleontologists have used debatable concepts, this says nothing about the potential of fossils themselves if analyzed properly. In a discussion covering several of these points, Schaeffer et al. (1972) claim that horse phylogeny could be reconstructed by treating all known living and fossil taxa as if they came from one time plane, so that the information that *Hyracotherium* is Eocene and *Equus* is extant is therefore superfluous. However, since all horses except *Equus* are extinct, this is quite different from saying that fossils are of no value in reconstructing phylogeny.

An analysis that seems to us more directly damaging to the view that fossils are valuable in reconstructing phylogeny was presented by Patterson (1981). Like Hennig (1966), Patterson argues that fossils might sometimes be expected to change ideas on homology or polarity within living groups, and to reveal details of the sequence of origin of features that characterize them. However, after consideration of a series of examples he concludes that in practice “instances of fossils overturning theories of relationship based on Recent organisms are very rare, and may be nonexistent” (p.218). It should be noted that almost all of his discussion deals with the effect of fossils on topologies of cladograms and therefore classification; he says less about their effects on ideas of character evolution, which might have as much or more interest for an understanding of evolutionary processes and adaptive factors involved in the origin of major groups (i.e.,

scenarios: Eldredge, 1979). Patterson's (pers. comm., 1980) discussion is of particular interest to us because among other examples he cites C.R. Hill as confirming that these conclusions hold for plants.

Although we agree with much of Patterson's discussion, his claim that fossils have had little impact on ideas of plant relationships seems counterintuitive from a historical point of view, especially when non-angiospermous groups are considered. It could be argued that one of the first major paleobotanical discoveries of this century, the recognition of seed ferns (Oliver and Scott, 1903), did not have much effect on phylogenetic concepts. These fossils seemed to fit the idea that seed plants are related to ferns, which was strongly promoted at about the same time on primarily neontological grounds by Jeffrey (1902, 1910), who combined the two groups in his class Pteropsida. However, the work of Florin (1938–1945, 1951) on Paleozoic cordaites and conifers was required to eliminate once and for all ideas that conifers were related to lycopsids, although the same homologies of conifer cones had been inferred by some morphologists. The concept of a close relationship between ferns and seed plants began to lose favor with recognition of the Devonian "progymnosperms" (Beck, 1960, 1970, 1981), which show that gymnospermous anatomy was acquired before seeds or fern-like fronds. Studies of progymnosperms were taken to support the already existing idea that the two widely recognized subgroups of seed plants, cycadopsids and coniferopsids, were separately derived from ancestors without seeds, since the progymnosperm *Archaeopteris* shows coniferopsid-like advances that cycadopsids and aneurophytalian progymnosperms lack. More recently, however, recognition of conifer-like features such as platyspermic seeds and saccate pollen in the Late Carboniferous seed fern *Callistophyton* led Rothwell (1982) to propose instead that conifers (and possibly other coniferopsids) were derived from platyspermic seed ferns by a radical shift in leaf morphology and habit, perhaps mediated by heterochronic sub-

stitution of scale leaves (cataphylls) for fronds.

It is less clear that fossils have had important effects on ideas of angiosperm phylogeny. Traditionally, the view that fossils provide the only definitive evidence on phylogeny has been widespread among angiosperm systematists, but they have used fossils very little in practice because of the supposedly uninformative nature of the early angiosperm record, which was believed to show the simultaneous appearance of diverse taxa in the Early Cretaceous. Together, these perceptions have often led to a dismissal of phylogeny in general as idle speculation. The discovery of bisexual flowers in Mesozoic Bennettitales led Arber and Parkin (1907) to propose a relationship between Bennettitales and angiosperms and to support the "euanthial" concept of angiosperm evolution: that showy, insect-pollinated, bisexual flowers with numerous free parts, as in *Magnolia*, are primitive in angiosperms, and that the apetalous, wind-pollinated, unisexual flowers of the Amentiferae, considered primitive by Von Wettstein (1907) and many members of the "Englerian" school, were derived by reduction and aggregation. However, Arber and Parkin's views on Bennettitales have subsequently been largely abandoned. The euanthial concept was already widespread and it has persisted, but it has been defended on other grounds, for example the association of euanthial floral structure with features such as vesselless wood and monosulcate pollen, whose primitive status was inferred from their almost universal occurrence in living as well as fossil gymnosperms. Cretaceous paleobotanical studies have caused excitement in showing trends in pollen and leaf morphology consistent with the primitive status of magnoliids and in elucidating the timing of early angiosperm evolution (Doyle, 1969, 1978; Muller, 1970, 1981; Hickey and Doyle, 1977; Upchurch, 1984). However, it can be argued that these studies have largely confirmed phylogenetic ideas already assumed by most students of modern angiosperms, and that they have not changed the views of supporters of unorthodox theories (e.g., Meeuse, 1972). A possible exception concerns the subclass Hamamelididae of

Cronquist (1968) and Takhtajan (1969), which includes both "core" members of the former Amentiferae with basically triporate pollen (Juglandaceae, Betulaceae, Myricaceae, Urticales, etc.) and groups with more primitive tricolpate pollen (*Trochodendron*, Hamamelidales, etc.). The Late Cretaceous Normapolles pollen complex appears to provide a link between triporate amentiferous pollen and triangular tricolporate pollen characteristic of the subclass Rosidae, a concept confirmed by discovery of Normapolles pollen in situ in juglandalian flowers (Friis, 1983). This suggests that the Hamamelididae are polyphyletic: the triporate Amentiferae are actually rosids, only very distantly related to the tricolpate groups (Wolfe et al., 1975; Hickey and Doyle, 1977). However, even this example is unclear: Wolfe (1973) had inferred that Juglandaceae are rosids based on the leaf architecture of extant members (although he did not extend this to other Amentiferae because of conflicting similarities between leaves of Betulaceae and Hamamelidaceae), and it has not been widely accepted by students of living plants (e.g., Cronquist, 1981).

In the present paper, we will not attempt to resolve the philosophical issues involved in the controversy over the role of fossils, nor to analyze in detail the historical role of paleobotany in plant phylogeny. Instead, we have adopted an experimental approach to the problem, using numerical cladistic methods to probe the effects of fossil taxa on both cladogram topology and hypotheses of character evolution. The only comparable study that we know was recently conducted by Gauthier, Kluge, and Roe (pers. commun., 1985), stimulated by a cladistic study of amniotes by Gardiner (1982), which emphasized extant groups. Gardiner's study led to the conclusion that birds and mammals are more closely related to each other than either is to any living group of "reptiles". This contrasts sharply with the view of most paleontologists that mammals are derived from (nested within) Permo-Triassic therapsids, whereas birds are derived from Mesozoic archosaurs (specifically dinosaurs), making their closest living rela-

tives the crocodylians. Using numerical cladistic methods, Gauthier et al. obtained results similar to Gardiner's when they analyzed modern groups only, but when they added fossil groups and osteological characters that they provide, cladograms corresponding to the classical view became more parsimonious. This appears to be a direct contradiction of Patterson's (1981) contention.

Our approach differs somewhat from that of Gauthier et al. in that we began with a data set amassed for a numerical cladistic analysis of both living and fossil seed plants and progymnosperms (Doyle and Donoghue, 1986). We then modified this matrix by subtracting and re-adding fossil groups, including both extinct relatives (outgroups) of the clade made up of all living seed plants and extinct seed plant taxa (belonging to the ingroup), with characters subtracted or re-added where appropriate. Essentially, these experiments ask what difference it would make to a hypothetical cladist if particular fossil groups were or were not known. This approach is not precisely analogous to Patterson's (1981), which emphasized comparisons of pre-Darwinian and molecular- or cytological-based classifications with classifications influenced by knowledge of fossils. However, we believe that our approach addresses the central issue more directly. With Patterson's approach, it is easy to dismiss contradictions between the two sorts of classifications on the grounds that the neontological classifications were poorly constructed in the first place. In order to avoid confusion of issues, we will not address the role of stratigraphy in polarity assessment; all of our decisions on polarity are based on outgroup comparison. Throughout our discussion, we will attempt to relate our results to macroevolutionary problems by considering their implications for adaptive scenarios and evolutionary processes involved in the origin of groups, with particular emphasis on coniferopsids, Gnetales, and angiosperms. Finally, we will attempt to make some generalizations on recognition of cases where fossil evidence is more or less critical for inference of relationships.

Data and methods of analysis

In the analysis of living and fossil groups on which the present study is based (Table I), we used two similar programs: the Wagner parsimony algorithm in PHYSYS (Mickevich and Farris, 1982), and the Mixed Method parsimony algorithm with the Wagner option in PHYLIP (Felsenstein, 1985), with global branch-swapping. Both algorithms begin with a matrix of binary characters, scored 0, 1, and X (missing information, coded 9 in PHYSYS and ? in PHYLIP), and attempt to find the tree(s) requiring the smallest number of character state changes (steps), treating forward changes and reversals equally. Since one of our main purposes was to evaluate the relative merits of current hypotheses, and since we wished to overcome problems of previous cladistic studies of seed plants (Hill and Crane, 1982; Crane, 1985), which omitted many characters that might support alternative results and coded others in ways that seemed to make restrictive assumptions on homology, we made

every attempt to include as many potentially useful characters from all organs as possible and to code certain controversial characters in ways consistent with alternative hypotheses (Tables II and III). For instance, we coded platyspermic seeds X1, so that they can be derived by one step from no seeds (00), as in Beck's (1970, 1981) hypothesis that cycadopsids and coniferopsids were derived from different groups of progymnosperms, and from radio-spermic seeds (10), as under Rothwell's (1982) hypothesis that conifers were derived from *Callistophyton*-like seed ferns. Likewise, we coded the linear-dichotomous leaves of coniferopsids as X01, derivable by one step from either the progymnosperm condition (000) or the seed fern one (100). We attempted to evaluate alternative hypotheses by adding "dummy" synapomorphies to the matrix to force particular groups together and then subtracting the corresponding numbers of steps after analysis, or by employing the user tree option in PHYLIP, which allows one to specify whole trees and determine their length.

TABLE I

Terminal taxa used (Doyle and Donoghue, 1986), with abbreviations used in figures

Taxa	Abbreviation
<i>Aneurophyton</i> s. lat., including <i>Triloboxylon</i> and <i>Eospermatopteris</i>	An
<i>Archaeopteris</i> s. lat., including <i>Svalbardia</i>	Ar
Early Carboniferous protostelic lyginopterids with multiovulate cupules	ML
"Higher" lyginopterids, including <i>Heterangium</i> and <i>Lyginopteris</i>	HL
<i>Medullosa</i> , not including <i>Quaestora</i> and <i>Sutcliffia</i>	Md
<i>Callistophyton</i>	Ca
Glossopteridales	G1
<i>Peltaspermum</i> (<i>Lepidopteris</i> , <i>Antevsia</i>)	Pl
Corytospermaceae (<i>Dicroidium</i> , <i>Rhexoxylon</i> , <i>Umkomasia</i> , <i>Pteruchus</i>)	Cs
<i>Caytonia</i> (<i>Sagenopteris</i> , <i>Caytonanthus</i>)	Ct
Cycadales, including Nilssoniales	Cy
Bennettitales (= Cycadeoidales)	Bn
<i>Pentoxylon</i>	Pn
Euramerican cordaites, including <i>Cordaites</i> , <i>Cordaianthus</i> , and <i>Mesoxylon</i>	Cd
Ginkgoales, including <i>Baiera</i> , <i>Karkeniania</i> , and <i>Ginkgo</i>	Go
Coniferales, including Lebachiaceae, Podocarpaceae, and Taxaceae	Cn
<i>Ephedra</i>	Ep
<i>Welwitschia</i>	We
<i>Gnetum</i>	Gn
Angiosperms	Ag

TABLE II

Characters used (Doyle and Donoghue, 1986). Throughout, 0 is used for the presumed ancestral state, 1 for the derived state, and X for missing information (also used in multistate characters for states where the precursor state is unknown). When only one state is listed in the definition of a character, it is the derived state

-
1. 0 = branching apical; 1 = axillary
 2. 0 = axillary buds single; 1 = multiple
 3. Leaves on (homologs of) progymnosperm penultimate order branches
 4. 0 = phyllotaxy spiral; 1 = opposite-decussate or whorled
 - 5-7. 000 = simple, dichotomous leaves only; 100 = pinnately compound leaves and cataphylls; 110 = simple, pinnately veined leaves and cataphylls; X01, XX1 = pointed cataphyll-like leaves only, or simple, linear or dichotomous leaves and cataphylls
 8. 0 = rachis regularly bifurcate; 1 = usually or always simple
 - 9, 10. 00 = one order of laminar venation, open; 10 = one order of laminar venation, reticulate; 11 = two or more orders of laminar venation, at least finest order reticulate
 11. 0 = poles of guard cells raised; 1 = level with aperture
 12. 0 = stomata entirely haplocheilic; 1 = some or all syndetocheilic
 13. Apical meristem with differentiation of tunica and corpus
 - 14, 15. 00 = protosteles (including vitalized types); 10 = eustele usually with external secondary xylem only; X1 = eustele with regular internal secondary xylem
 16. 0 = some or all stem bundles mesarch or exarch; 1 = all endarch
 - 17, 18. 00 = leaf traces from one stem bundle or protoxylem strand (one-trace unilacunar node); 10 = from more than two bundles (multilacunar node); X1 = from two adjacent bundles (two-trace unilacunar node)
 19. 0 = some scalariform pits in metaxylem; 1 = no scalariform metaxylem, circular bordered pits in protoxylem
 20. 0 = only circular bordered pitting or perforations in secondary xylem; 1 = at least some scalariform
 21. Vessels in the secondary xylem
 22. 0 = rays uniseriate or rarely biseriata; 1 = at least some multiseriate
 23. Secretory canals
 24. Mäule reaction
 - 25-27. 000 = dichotomous megasporangiate fertile appendages (cupules) on radial axis; 100 = pinnately compound megasporophyll; 110 = once-pinnate megasporophyll, with two rows of simple leaflets or cupules bearing ovules; X01, XX1 = ovule on one-veined megasporophyll or sessile
 - 28-30. 000 = dichotomous microsporangiate fertile appendages on radial axis; 100 = pinnately compound microsporophyll; 110 = once-pinnate microsporophyll, with two rows of simple leaflets or stalks bearing pollen sacs; X01, XX1 = one-veined microsporophyll
 31. 0 = ovule on lateral appendage; 1 = terminal
 32. 0 = homologs of progymnosperm fertile branchlets on homologs of lower order axes; 1 = on homologs of last order axes
 - 33-35. 000, 010 = ovule(s) in radial cupule; 100 = ovules directly on more or less laminar sporophyll (terminal, abaxial, or adaxial); 110 = ovules in anatropous cupule, or anatropous and bitegmic; X01 = ovule with second integument derived from two appendages lower on axis
 36. 0 = several ovules per anatropous cupule or potential homolog; 1 = one
 37. 0 = microsporangia terminal, marginal, or adaxial; 1 = abaxial
 38. 0 = microsporangia free; 1 = fused at least basally into microsperangia
 39. 0 = microsporophylls spirally arranged; 1 = whorled
 40. 0 = strobili on undifferentiated axes, or only female aggregated into compound strobili; 1 = both male and female strobili aggregated
 - 41, 42. 00 = no seeds; 10 = radiospermic seeds; X1 = platyspermic seeds
 - 43, 44. 00 = megasporangium with unmodified apex; 10 = lagenostome with central column; 11, X1 = pollen chamber without central column
 45. Micropylar tube
 46. Nucellar vasculature
 47. 0 = nucellar cuticle thin; 1 = thick, maceration-resistant
 48. Heterospory
 - 49, 50. 00 = tetrad scar, no sulcus/pollen tube; 10 = sulcus/pollen tube; 11 = pollen tube but no sulcus
 51. 0 = pollen radially symmetrical or mixed; 1 = strictly bilateral
-

TABLE II (continued)

52.	0 = pollen nonsaccate or subsaccate; 1 = saccate
53.	0 = infratectal structure alveolar; 1 = granular or columellar
54.	Pollen striate
55.	0 = megaspore tetrad tetrahedral; 1 = linear
56.	0 = megaspore wall thick; 1 = thin or lacking sporopollenin
57.	0 = microgametophyte with prothallial(s) and sterile cell; 1 = with prothallial but no sterile cell
58.	0 = motile sperm; 1 = siphonogamy, nonmotile sperm
59.	0 = megagametophyte monosporic; 1 = tetrasporic
60.	Apex of megagametophyte free-nuclear or with multinucleate cells; wall formation irregular, resulting in polyploid cells at maturity; egg a free nucleus
61.	0 = early embryogenesis free nuclear; 1 = entirely cellular
62.	Embryo with feeder

TABLE III

Data matrix for extant and fossil taxa (Doyle and Donoghue, 1986)

	1	2	3	4	5	6
Aneurophyton	0X00000X00XXX0000000000X000000X0000X000000000XX000000000X00XXX					
Archaeopteris	0X10000X00XXX100000000X0000000X1000X000000000XX100000000X00XXX					
Multiov. lyg.	XX0010000000X0000000010X00000000000X010X101000X10000X000X000XX					
Higher lygin.	100010000000X0000000010X10010000000X010X101000X10000X000X000XX					
Medullosa	100010000000XX101000011X10010000100X010X101101X1001000X0X0X0XX					
Callistophyton	1000100100X0X1000000010X100100001000110XX11100X1101100X00XX0XX					
Glossopterids	10X0110X10X0X10XXX0000XXX0XX000X0000000XX1X10011101101X0XXX0XX					
Peltaspermum	XX0X100100X0XXXXXXXXXXXXX110100001000100XX111XX011010X0X0XXXXXX					
Corystosperms	XX0010000000XX101000000X100110001101100XX111XX011011X0X1XXXXXX					
Caytonia	1000100X1010XXXXXXXXXXXXX110100001100X10XX1110011101100X1XXXXXX					
Cycads	XXX0110X00000101100001101X01X00X100X100X10X1010110100010000000					
Bennettitales	10X0110X0001X1010001011XXX11100X010X0110XXX110X110101011XX00XX					
Pentoxylon	10X0110X0000XX1XX101010XXX10100X010X0X10X1X100111010X0X1XXXXXX					
Cordaites	1010X01X0000X1000000000XX01X0101X00X0001X1X10XX1000100X000X0XX					
Ginkgos	1010X01X00000101X1100000X01X0101X00XX000X1X1000110100010000000					
Conifers	1010X01X0000010100100010X01X0101X00X1000X1X1000100110010000000					
Ephedra	11X1XX1X00001101X1101101XX1XX11XX01X0111X1X11001110111010000					
Welwitschia	11X1XX1X11010101X1101111XX1XX11XX01X0111X1X11001101011X111111					
Gnetum	11X1110X11011101101X1101XX1XX11XX01X0X1110X11001110010X1111111					
Angiosperms	10X0110X111111011001X1011101100X1101X100XXX001110101011X10010					

Finding most parsimonious trees with both programs requires considerable experimentation. Because the number of possible trees increases rapidly with increasing numbers of taxa (Felsenstein, 1978), present methods cannot guarantee finding the most parsimonious tree(s) with large data sets. In Wagner algorithms, taxa are added sequentially to the analysis in the most parsimonious position, and what trees are found depends in part on the order of entry of taxa. PHYSYS determines

the order of entry based on an advancement index, but with PHYLIP the order of entry is specified by the user. The shortest trees that we obtained with PHYSYS (124 steps) were found only by forcing together taxa with dummy characters. Several of our shortest trees (123 steps) were obtained with PHYLIP, by judicious shuffling of the order of entry of taxa (as recommended by Felsenstein in the on-line PHYLIP documentation), and by use of the user tree option. In general, we obtained the

best results by entering taxa roughly in order of increasing advancement, but placing possible alternative "linking" taxa in various arrangements before specialized and problematical ones. We emphasize that this required much familiarity with the data and potential alternative arrangements of groups, many of which were first seen during experimentation with PHYSYS. Other 123-step trees were kindly brought to our attention by W.E. Stein (pers. commun., 1986), using the PAUP program of D.L. Swofford.

One of our most parsimonious trees is shown in Fig.1; others differ in reversing the order of Bennettitales and *Pentoxylon* and/or rearranging *Callistophyton*, coniferopsids, corystosperms, and cycads in various ways. In general, our trees are similar to the preferred tree of Crane (1985). Arranged sequentially from the base are the progymnosperms *Aneurophyton* and *Archaeopteris*, two groups of Carboniferous lyginopterid seed ferns, the Late Carbon-

iferous seed fern *Medullosa*, and a major clade that includes all extant groups, initially united by platyspermic seeds and saccate pollen, within which *Callistophyton* has the largest number of primitive traits. Cordaites, conifers, and ginkgos form a group at (or near) the base of this clade; this result supports Rothwell's (1982) hypothesis that conifers were derived from platyspermic, saccate seed ferns rather than *Archaeopteris*-like progymnosperms (Beck, 1970, 1981), but it implies that this concept should be extended to coniferopsids as a whole (cf. Crane, 1985). In Fig.1 cycads are associated with the Permo-Triassic seed fern *Peltaspermum*, not with medullosans as often suggested (e.g., Crane, 1985); with this arrangement it is most parsimonious to interpret cycads as secondarily radiospermic, which is consistent with the fact that seeds of Permian taeniopterids considered primitive cycads by Mamay (1976) appear to be flattened and *Cycas* seeds have bilateral symmetry (interpreted as sec-

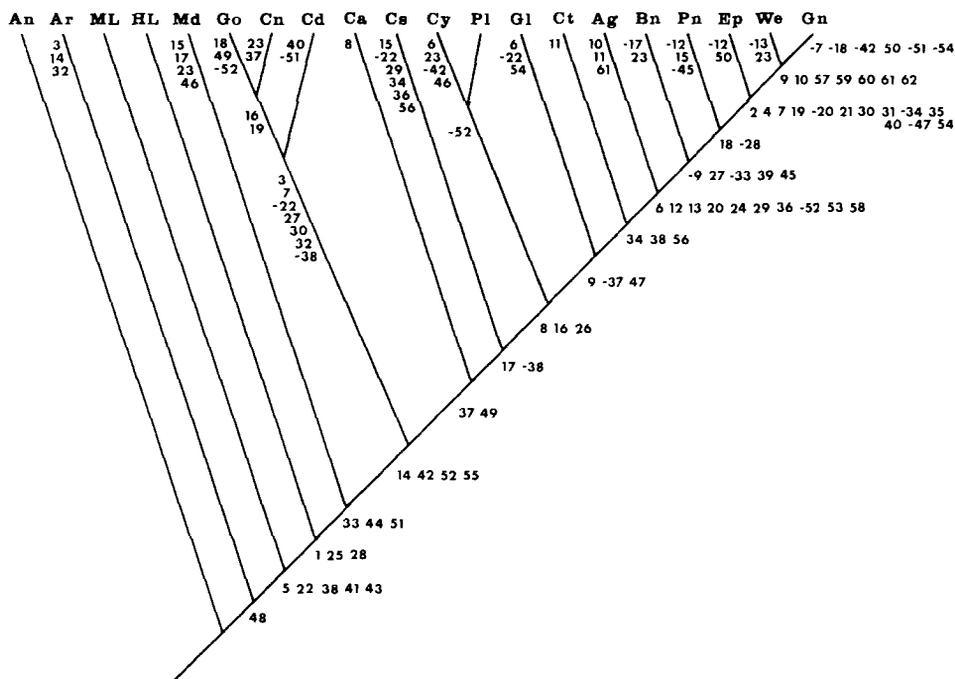


Fig.1. One of several most parsimonious 123-step trees derived from analysis of the whole data set (Doyle and Donoghue, 1986). Taxa and their abbreviations are defined in Table I; characters in Table II. Minus signs before characters indicate reversals.

ondary by Meyen, 1984). However, in other 123-step trees cycads are linked with *Medullosa* or form the sister group of the platyspermic clade. The angiosperms also belong in the platyspermic group, forming a clade with Bennettiales, *Pentoxylon*, and Gnetales; since all four groups have flower-like reproductive structures, we refer to them as the anthophytes. Crane (1985) recognizes the same clade and connects it with the Mesozoic seed ferns (corystosperms, *Caytonia*, glossopterids), based largely on the hypothesis that the reflexed cupule of Mesozoic seed ferns is homologous not only with the anatropous bitegmic ovule of angiosperms (Gaussen, 1946; Stebbins, 1974; Doyle, 1978) but also with the orthotropous cupulate ovule of Bennettiales and *Pentoxylon*. All of our most parsimonious trees differ from Crane's in relating anthophytes more closely to *Caytonia* and glossopterids than to corystosperms, and in treating angiosperms as the sister group of other anthophytes, rather than linked directly with Gnetales.

Implications of our results for evolution of key characters in seed plants are summarized in Fig. 2, with less favored relationships indicated by dotted lines. On a broad scale, our most parsimonious trees imply that there were two trends in seed plants from a "cycadopsid" to a "coniferopsid" habit, one in the Carboniferous leading to the coniferopsids and the other in the Mesozoic leading to Gnetales. Elsewhere we argue that both trends may be tied to a shift to drier habitats (Doyle and Donoghue, 1986). Although our results indicate that Gnetales are the closest living relatives of angiosperms, they in no way support suggestions that angiosperms were derived from a gnetalian prototype, as in Von Wettstein's (1907) theory that the catkins of Amentiferae are homologous with gnetalian compound strobili and that bisexual flowers originated by aggregation of unisexual units. Rather, they are more consistent with the views of Arber and Parkin (1907, 1908), who proposed that angiosperms, Bennettiales, and Gnetales were derived from a common ancestor with bisexual flowers and that the flowers of

Gnetales and Amentiferae were secondarily reduced and aggregated. Our trees imply that the first anthophytes had pinnate mega- and microsporophylls, but the megasporophylls were reduced to single ovules in the common ancestor of Bennettiales and Gnetales, whereas the microsporophylls were independently simplified in angiosperms and Gnetales.

Experiments show that some connections in this scheme are very strong, but others are weaker. For example, only one step is added if coniferopsids are associated with *Archaeopteris* (Beck, 1970, 1981), which would imply that the seed originated twice. The position of the anthophytes and relationships among members of the platyspermic clade are also relatively unstable: we found many trees only one step longer (124 steps) with cycads the sister group of the platyspermic clade, coniferopsids linked with *Peltaspermum* and/or glossopterids, and anthophytes linked with *Caytonia* and corystosperms, *Caytonia* and glossopterids, corystosperms alone, or all three groups in various orders (cf. Crane, 1985). Three extra steps are needed to link anthophytes with *Medullosa* and cycads. Most disconcertingly, we found trees of only 125 steps with anthophytes nested in the coniferopsids, with Gnetales the sister group of angiosperms, *Pentoxylon*, and Bennettiales, suggesting that the latter groups originated from coniferopsids via Gnetales-like intermediates (a "neo-englerian" arrangement). On the other hand, the anthophytes appear to be a more robust group. Moving Gnetales (the least securely associated group) into the coniferopsids, their next-best position, adds four steps, and other arrangements that break up the anthophytes are still less parsimonious. Angiosperms can be linked directly with *Caytonia* with addition of only one step, but in this case the two groups are still most closely associated with other anthophytes.

In the present study, all analyses were performed with PHYLIP (version 2.8), using an Eagle PC microcomputer. For data sets with larger numbers of taxa, we used the Wagner option in the Mixed Method Parsimony algorithm, as discussed above. When the number of

taxa was small (up to nine), we used the Wagner option in the Penny algorithm in PHYLIP, which uses a "branch and bound" search strategy (Hendy and Penny, 1982) that guarantees finding all most parsimonious trees (with larger numbers of taxa, the search time becomes prohibitively long). We tested alternative hypotheses by means of the user tree option and/or the dummy character method discussed above.

With PHYLIP, trees can be rooted either by specifying one of the included taxa as outgroup to the rest or by specification of a set of ancestral states (0, 1, or X). In experiments with the whole data set and subtraction of fossil taxa, we rooted trees by specifying *Aneurophyton* (which by comparison with outgroups appears to be primitive in all characters considered) as the outgroup, but in experiments with the modern data set and addition of fossils to it we used the ancestral states option, specifying primitive states on the basis of various concepts of outgroup relationships (as discussed further below). When the ancestral states option is invoked, the program provides the most parsimonious "best guesses of ancestral states" for all characters (which may of course still be X), given the rooting defined by those characters that were polarized. We used this feature extensively in evaluating the implications of knowledge of fossil groups for character evolution.

In compiling characters for our previous study, we consistently eliminated autapomorphies (where the derived state is limited to one taxon), since they provide no information on cladistic relationships of groups and give a misleading impression of the amount of data supporting a scheme. In the present study we followed a somewhat different procedure. In all experiments we eliminated characters that were invariant in the subset of taxa represented, and in experiments involving subtraction of fossil groups from the whole data set we also eliminated autapomorphies, since polarities were the same as with the whole data set, being determined by *Aneurophyton*. However, in experiments based on modern groups only,

or on addition of fossils to modern groups, we left in all varying characters even when the original derived state occurred in only one taxon, since in these experiments polarities of many characters become equivocal or are even reversed, depending on the rooting. The most complex decisions concerned recoding of multistate characters, where some but not all states disappear or become autapomorphic with subtraction of groups; as discussed in individual experiments, we attempted to recode such characters in the light of information that could be obtained from the groups included in the analysis.

Experiments

Analyses of extant groups only

Our first experiments were designed to assess whether and to what extent fossils clarify seed plant phylogeny by providing closer extinct relatives (outgroups) of extant seed plants as a clade (the ingroup). As argued by Maddison et al. (1984), addition of closer outgroups may require changes in ideas on polarity and therefore relationships in the ingroup, and this should hold whether the outgroups are living or fossil. Outgroups could have been entered into the analysis as additional taxa and ingroup and outgroup relationships resolved simultaneously. However, because we wished to consider particular sets of outgroups separately and to keep the total number of taxa small enough to use the Penny algorithm, we instead employed the two-step outgroup procedure described by Maddison et al. (1984), using different outgroup arrangements to assess character states of a hypothetical ancestor, and then using the resulting list of states to root the ingroup tree with the ancestral states option. If one of the two character states (0, 1) found in the ingroup is found in both of the two nearest outgroups, it is most parsimonious to assume that that state occurred in the hypothetical ancestor, but if the first two outgroups differ in state and additional outgroup information is unavail-

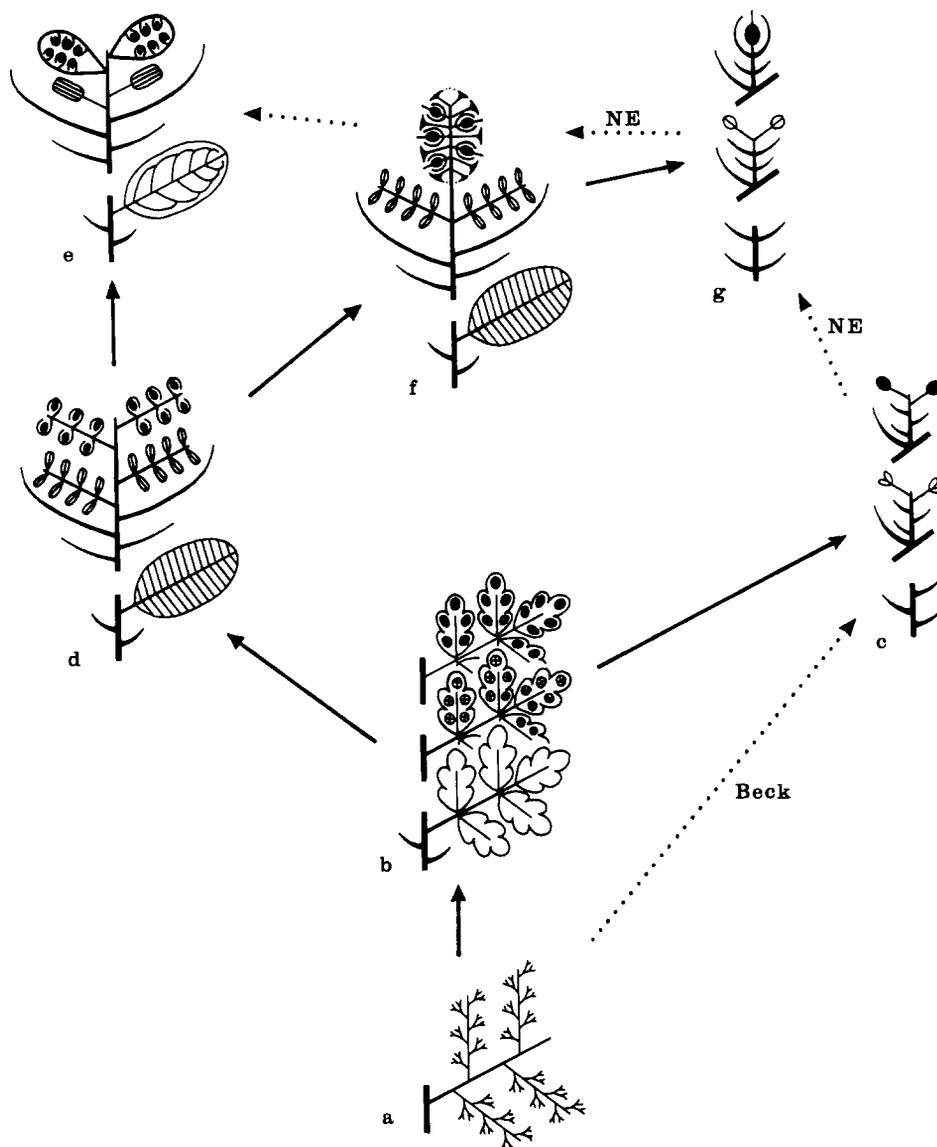


Fig.2. Major transformations in leaf morphology and reproductive structures of seed plants inferred from the cladogram shown in Fig.1. Groups indicated: (a) progymnosperms; (b) seed ferns; (c) primitive coniferopsids; (d) hypothetical common ancestor of anthophytes (angiosperms, Bennettitales, *Pentoxylon*, Gnetales); (e) angiosperms; (f) Bennettitales; (g) Gnetales. Less parsimonious alternative transformations are indicated with dotted lines ("Beck": independent derivation of cycadopsids and coniferopsids from progymnosperms; "NE": a "neo-englerian" arrangement, with anthophytes nested in coniferopsids).

able, the ancestral state for the character is equivocal and is thus coded X.

Removal of the 13 fossil taxa from the 20 groups in our original analysis resulted in reduction of 62 characters to 40 (Table IV).

Many characters become invariant in the taxa remaining and were therefore eliminated (e.g., axillary branching, endarch primary xylem, heterospory). Some multistate characters collapse to binary characters (e.g., lagenostome

TABLE IV

Experiments with extant taxa. "Conservative" through "seed fern" designate sets of user-specified ancestral states based on different assumptions concerning outgroup relationships. "BGAS" represents "best guesses" of ancestral states provided by PHYLIP for the most parsimonious trees obtained with the conservative rooting

	1	2	3	4	5	6
Conservative	-0-0--X-0-100---000X0XX0--X--XX--XX-XXX0-X--XXX--XXXXX-0000010					
Moderate fern	-0-0--0-0-100---000X0XX0--0--00--XX-XX00-X--XXX--XXXXX-0000010					
Extreme fern	-0-0--0-0-100---000101X0--0--00--XX-XX00-X--XXX--XXXXX-0000010					
Progymnosperm	-0-0--1-0-100---00000000--1--10--X0-0000-X--XXX--X0000-0000010					
Seed fern	-0-0--0-0-000---X00001X0--0--00--X0-0100-0--0XX--XX000-00000X0					
Cycads	-X-0--0-0-000---10000110--0--00--00-100X-0--010--01000-0000000					
Ginkgos	-0-0--1-0-000---X1100000--1--10--00-X000-1--000--01000-0000000					
Conifers	-0-0--1-0-000---00100010--1--10--00-1000-1--000--01100-0010000					
Ephedra	-1-1--1-0-001---X1101101--1--11--01-0111-1--100--11011-1010000					
Welwitschia	-1-1--1-1-010---X1101111--1--11--01-0111-1--100--01011-1111111					
Gnetum	-1-1--0-1-011---101X1101--1--11--01-0X11-0--100--10010-1111111					
Angiosperms	-0-0--0-1-111---1001X101--0--00--10-X100-X--001--01010-1X10010					
BGAS, tree 4a:	-0-0--X-0-100---00000XX0--X--X0--00-1000-1--000--01000-0000010					
BGAS, tree 4f:	-0-0--X-0-100---000001X0--X--X0--00-??00-1--000--010?0-0000010					

vs. normal pollen chamber), or it becomes unlikely that distinctions made with the whole data set would be recognized. For example, with the loss of groups with simply reticulate venation (*Caytonia*, glossopterids), two characters that appear distinct with the whole data set, reticulate venation and presence of several vein orders, are invariably associated and would probably be interpreted as redundant, so they were combined as a single character. We eliminated two characters that express advances of *Archaeopteris* over *Aneurophyton* in the arrangement of the leaves (3) and fertile appendages (32); if coniferopsids are interpreted in a progymnosperm context, it is clear that they have the *Archaeopteris* state in these characters, but without reference to progymnosperms these characters are less obvious as a basis for linking coniferopsids with each other. With the loss of groups with dichotomous leaves and no cataphylls (progymnosperms) and pinnately compound leaves (seed ferns), only two main leaf conditions remain: simply pinnate (cycads, angiosperms, and *Gnetum*) and linear-dichotomous (conifers, *Ginkgo*, *Ephedra*, *Welwitschia*). Distinctions might be made within these categories, for instance

between the dissected leaves of cycads and the entire leaves of angiosperms and *Gnetum*, but ordering the resulting states would be problematical. Cycad leaves might be considered more fern-like in being dissected, but they are basically once-pinnate, with leaflets that have parallel-dichotomous venation, whereas most fern leaves are several-times compound, with pinnules that themselves have pinnate venation. In such cases, we have assumed that a hypothetical investigator who knew only extant groups would prefer to err on the side of caution and keep the number of distinctions to a minimum. This entails little loss of information, since the special similarity between the leaves of angiosperms and *Gnetum* is expressed by the venation character. We assumed (perhaps optimistically) that the angiosperm stamen would be recognized as a basically pinnate structure because the pollen sacs are arranged as lateral pairs, in contrast to the situation in coniferopsids and Gnetales. In order to keep this an exercise based on Recent information only, we rescored conifers as having a sulcus and pollen tube and siphonogamy, although the earliest Paleozoic conifers had a tetrad scar and no sulcus and presum-

ably had motile sperm (Mapes and Rothwell, 1984).

An unrooted analysis of the modern data set gave three unrooted trees ("networks") of 57 steps (Fig.3). One (Fig.3.a) is consistent with all the shortest trees obtained from the whole data set (e.g., Fig.1), as well as with the rooted trees obtained most frequently in analyses of the modern data set with the various rootings described below (Fig.4.a, f). The other two (Fig.3.b, c) are consistent with "neo-englerian" rooted trees (among others), with both angiosperms and Gnetales nested in coniferopsids (e.g., Fig.4.d), which are less parsimonious than the shortest rooted trees obtained with both modern and complete data sets. Meacham (1984) argues that it is best to construct an unrooted tree first and then attempt to root it rather than to begin with assumptions on polarity. However, this example shows that unrooted analysis may produce some networks that are globally less parsimonious under any reasonable outgroup assumptions, so that even minimal a priori polarity assessment is of value in reducing the number of alternatives to be considered and should therefore be attempted (cf. Donoghue and Maddison, 1986).

Altogether, we did five sets of exercises with the extant data set, with rootings based on different assumptions on outgroup relationships (Table IV). The first or "conservative" rooting represents what we consider the strongest conclusions on polarity that could be drawn from extant outgroups only, assuming that ferns and sphenopsids are closer to seed plants than lycopsids (for reasons discussed below) but not specifying more detailed relationships. The second and third rootings explore the historically important view that seed

plants were derived from (nested within) ferns, expressed in the widely adopted grouping of the two taxa into Pteropsida (Jeffrey, 1902, 1910): a relatively cautious "moderate fern" rooting and an "extreme fern" rooting based on more questionable homologies between ferns and seed plants. The last two exercises are the first tests of the effect of fossil data on seed plant phylogeny, using a "progymnosperm" rooting and a "seed fern" rooting. They model hypothetical situations in which we knew (1) about progymnosperms (*Aneurophyton*, *Archaeopteris*) but no other fossils, and (2) about the most primitive Carboniferous seed ferns ("lyginopterids" and *Medullosa*) but not progymnosperms, as was the case early in this century. Where information on characters in the fossil groups is lacking (e.g., Mäule reaction, embryology), we relied on living lower vascular plants as the next closest outgroups.

For each rooting, besides using the Penny algorithm to find all most parsimonious trees, we also determined the lengths of several user-specified trees that are of particular theoretical interest (Fig.4): (a) with coniferopsids the sister group of all other taxa and angiosperms related to Gnetales (consistent with both the most parsimonious tree of all groups shown in Fig.1 and the concept that coniferopsids and cycadopsids were separately derived from progymnosperms); (b) with coniferopsids and angiosperms plus Gnetales as sister groups, and with cycads the sister group of both (as in other most parsimonious trees derived from the whole data set and the trees of Crane, 1985); (c) with coniferopsids and cycadopsids as sister groups, but with Gnetales nested in coniferopsids; (d) a "neo-englerian" arrangement, with both angiosperms and Gnetales nested within

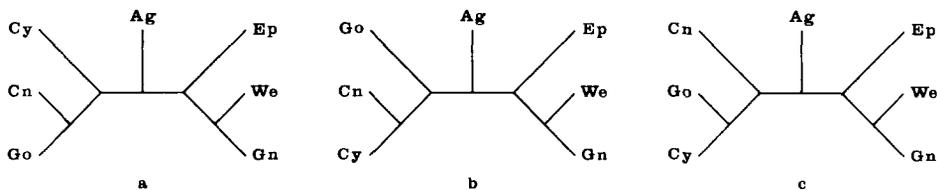


Fig.3. Most parsimonious unrooted trees (networks) obtained from analysis of extant seed plant taxa (57 steps).

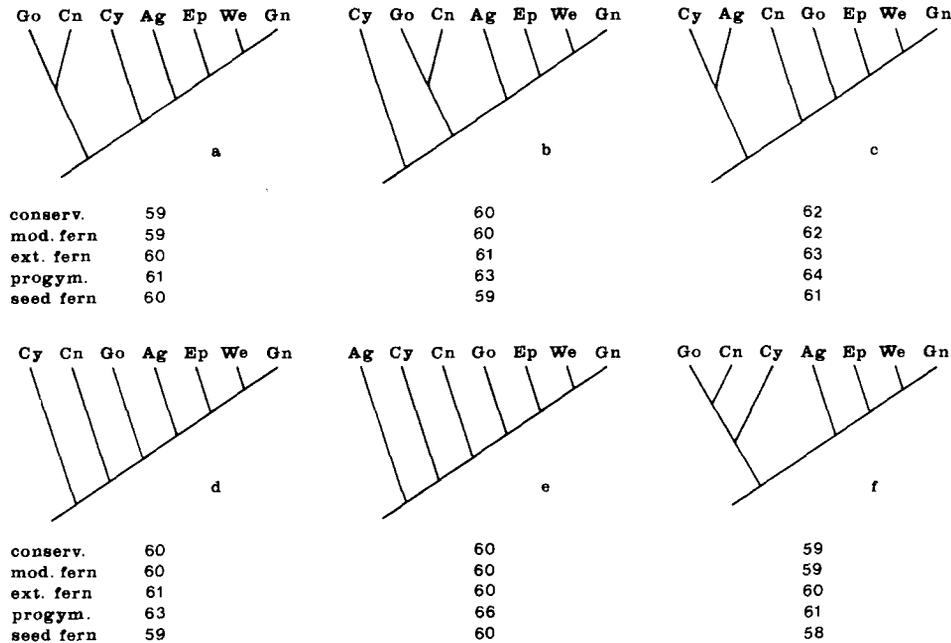


Fig.4. (a–e) User-specified trees of extant seed plant taxa, and (f) a topology seen among the most parsimonious trees obtained in all experiments, with the number of steps obtained using ancestral states based on different assumptions concerning outgroup relationships (see text).

the coniferopsids; and (e) with Gnetales nested in coniferopsids but with cycads the sister group of coniferopsids, making angiosperms basal. Figure 4 also includes a tree (Fig.4.f) that we found with all rootings, in which cycads are linked with coniferopsids and angiosperms with Gnetales.

Conservative rooting

Neontological evidence supporting the assumption made here that ferns and/or sphenopsids are closer to seed plants than lycopsids includes the fact that seed plants, ferns, and sphenopsids differ from lycopsids in having multiflagellate sperm, a derived feature on comparison with bryophytes and green algae (plus mesarch or endarch primary xylem and longitudinal sporangial dehiscence, characters of less certain polarity when only living groups are considered). Ferns and sphenopsids may form a clade, based on presence of peripheral loops in early fossil members of both groups

(Doyle and Donoghue, 1986), but since this is not evident from any modern data, we have treated ferns, sphenopsids, and seed plants as an unresolved trichotomy.

Under these assumptions, we reached the same decisions on the polarity of 16 characters as with the whole data set, because one of the states does not occur (or if present is clearly independently derived) in extant non-seed plants. Most of these are features now restricted to angiosperms, Gnetales, or both (e.g., opposite leaves, reticulate venation, syndetocheilic stomata, tunica layer in the apical meristem, vessels, Mäule reaction, compound strobili, reduced megaspore wall, siphonogamy, and other features associated with gametophyte reduction). In a great many other characters, we could find no basis for deciding which state was ancestral, either because the appropriate characters are lacking in the outgroups (e.g., features of secondary xylem, seeds), or because both states are present. For

example, both pinnately organized and linear-dichotomous leaves occur in the outgroups, secretory canals occur in some fern groups but not others, and both trilete and monolete spores (corresponding to radial and bilateral pollen symmetry) exist in ferns and lycopsids. In some cases, the comparisons that led us to leave the ancestral state undefined may seem farfetched (e.g., fused pollen sacs with synangia of Marattiales, whorled microsporophylls of Gnetales with sporangiophores of sphenopsids, inaperturate pollen with alete spores of *Equisetum*, or saccate pollen with the perinate condition in various lower groups), but in formulating this rooting we wished to give wide leeway to potential homology. In two cases, we reversed polarities assumed with the whole data set. There we assumed that flat guard cells (angiosperms, *Caytonia*) and cellular embryogeny (angiosperms, *Welwitschia*, *Gnetum*) were secondarily derived within seed plants, because guard cells with raised poles and large egg cells (correlated with free-nuclear embryogeny in modern plants, presumably for functional reasons) are characteristic of Carboniferous seed ferns and cordaites, which appear to be basal within seed plants on outgroup comparison with progymnosperms. However, flat guard cells and cellular embryogeny are ubiquitous in living lower vascular plants, so the elimination of evidence from fossil groups requires designating these states as ancestral.

Analysis of this data set yields two most parsimonious 59-step cladograms (Fig.4.a, f). Both agree with trees derived from the whole data set in showing coniferopsids (conifers plus *Ginkgo*) and Gnetales as natural groups, *Ephedra* as the sister group of *Welwitschia* and *Gnetum*, and angiosperms as the sister group of Gnetales. One (Fig.4.a) is consistent with the cladogram of extant and fossil groups shown in Fig.1, with coniferopsids the sister group of the remaining taxa and cycads the sister group of angiosperms plus Gnetales (anthophytes). However, in the other (Fig.4.f), cycads are the sister group of coniferopsids, an arrangement never seen with the whole data set. Further-

more, the alternative topology of extant groups derived from the whole data set, with cycads basal (Fig.4.b), is not seen (it is one step less parsimonious).

Consideration of the user-specified trees suggests that one effect of elimination of fossil groups is poorer resolution of alternatives that differ considerably in relative parsimony when fossils are included. Most significantly, one tree with Gnetales separated from angiosperms and nested in the coniferopsids (Fig.4.e) is only one step longer than the shortest trees, while with the whole data set moving Gnetales into the coniferopsids adds at least four steps. Nevertheless, the modern data set does allow rather strong rejection of some alternatives: trees with angiosperms forced into (derived from) Gnetales, as the sister group of *Welwitschia* and *Gnetum*, are five steps longer than the shortest trees, and trees with taxa forced into three major clades based on the scheme of Meyen (1984) — Ginkgoopsida (*Ginkgo*, *Ephedra*), Pinopsida (conifers), and Cycadopsida (cycads, angiosperms, *Welwitschia*, *Gnetum*), with the last two related to each other — are even worse (71 steps).

At first sight, the two 59-step trees might suggest the two major hypotheses on relationships of seed plant groups based on fossil evidence: Fig.4.a, the Beck hypothesis that coniferopsids and cycadopsids were separately derived from progymnosperms; Fig.4.f, the Rothwell hypothesis that conifers (extended to coniferopsids as a whole) were derived from a seed fern prototype. However, in fact they have no clear relation to these two hypotheses in terms of either topology (Fig.4.a is equally consistent with our analysis of the whole data set) or character evolution. This can be seen by examination of the "best guesses" of ancestral character states provided by PHYLIP (BGAS, Table IV) and the equally parsimonious placements of character state changes on each tree shown in Fig.5. For example, under both topologies it is equally parsimonious to assume that either pinnate or linear-dichotomous leaves are basic in seed plants (Fig.5.a, d vs. Fig.5.b, c, e). Since the concept that pinnate

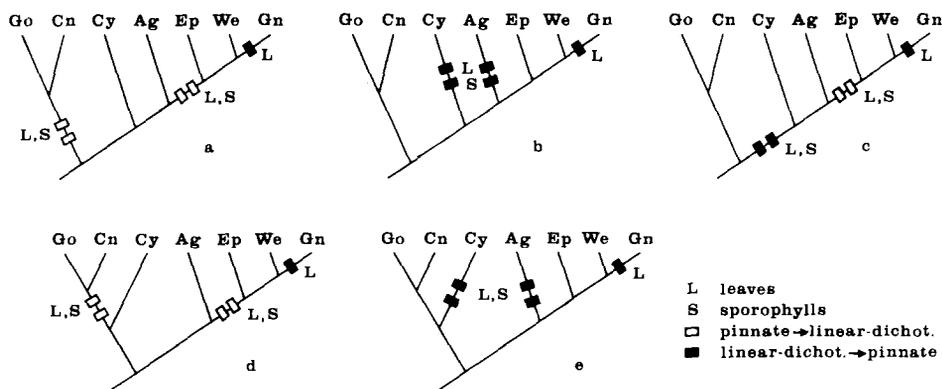


Fig.5. Selected equally parsimonious placements of the leaf and mega- and microsporophyll characters (7, 27, 30) on the two shortest trees obtained with the conservative rooting (Fig.4a, f; 59 steps).

leaves are ancestral (favored by analysis of the whole data set) implies that drastic leaf reduction occurred in both Gnetales and coniferopsids, possibly linked to a shift to arid habitats (Doyle and Donoghue, 1986), whereas the alternative concept does not, both trees permit a great range of adaptive scenarios. Furthermore, without indications (like those provided by *Archaeopteris*) that coniferopsids are related to one group of non-seed plants and cycadopsids to another, it is most parsimonious to assume that seeds are homologous in coniferopsids and cycadopsids even when they are sister groups, rather than originating twice, as under the Beck hypothesis (this is also true for axillary branching, eustele, pollen chamber, linear megaspore tetrad, and sulcus and pollen tube, which were eliminated from this data set). Interestingly, given both trees, Fig.4.a and f, it is most parsimonious to assume that the common ancestor of living seed plants had platyspermic seeds, as in Fig.1 and most other trees based on the whole data set; fossils are needed to show that their earlier ancestors were radiospermic.

Evolution of characters and corresponding scenarios within higher seed plant groups are also poorly defined. Since it is equally parsimonious to consider the pinnately organized leaves and sporophylls of angiosperms either primitive or derived relative to Gnetales,

Gnetales might have arisen from ancestors with more complex floral structures by reduction, as proposed by Arber and Parkin (1908) and supported by analysis of the whole data set, or angiosperms might have arisen from Gnetales-like ancestors with linear leaves and simple sporophylls (though not such gnetalian advances as opposite leaves and isolated circular-bordered pits in the protoxylem) by elaboration or aggregation of simple floral units, as proposed by Von Wettstein (1907). Without knowledge of Mesozoic seed ferns, the idea that the anatropous bitegmic ovule of angiosperms is a cupule derived from a reflexed leaflet might never be considered. Other concepts might appear equally plausible; we assumed that the development of the gnetalian outer integument from two perianth-like primordia (Martens, 1971) would be recognized as evidence that it is not homologous with the angiosperm outer integument, but this may have been overly optimistic.

Our experiments also suggest that ignorance of fossils may lead one to underestimate the amount of homoplasy in some characters. Thus analysis of the whole data set implies that saccate pollen existed in the common ancestor of all extant groups and was lost in the lines leading to cycads, *Ginkgo*, and anthophytes, but on extant data alone it would appear to be a conifer autapomorphy. In other cases, con-

vergences may be misinterpreted as synapomorphies. Even if vessels are assumed to be basic in angiosperms (Young, 1981), the trees derived from the whole data set imply that they originated independently in angiosperms and Gnetales, since they are absent in Bennettiales and *Pentoxylon*. However, given the trees based on extant taxa, if vessels are taken as basic in angiosperms, it is most parsimonious to assume that they are homologous in the two modern groups.

Fern rootings

Both "moderate" and "extreme" fern rootings assume that seed plants are nested within ferns, so that the first two outgroups are both fern taxa, without specifying exact relationships. In historical terms, this may be a more accurate representation of ideas not influenced by fossils than the previous rooting, since it was first articulated by Jeffrey (1902, 1910) on primarily neontological grounds and has fallen out of favor largely as a result of studies on progymnosperms and seed ferns (Beck, 1970), although Beck et al. (1982) argue that it should have been and was questioned on the basis of stelar anatomy of extant plants. In considering this alternative, we are not erecting a straw man: despite paleobotanical critiques, the idea that ferns are the closest relatives of seed plants is far from dead. In a synthesis of recent cladistic studies emphasizing extant groups, Bremer (1985) treats Ophioglossales, Marattiales and "true ferns", and seed plants as a trichotomy, united on megaphyllous leaves with a midrib (i.e., pinnate leaves) and trichomes. From a paleobotanical point of view, these characters are highly questionable as synapomorphies, since apparent fossil relatives of both seed plants (progymnosperms) and ferns (Cladoxylales, some coenopterids) have three-dimensional branch systems rather than pinnate fronds, and trichomes are rare in gymnosperms.

Both fern rootings differ from the conservative rooting in assuming that pinnate leaves and sporophylls are ancestral, and terminal ovules and whorled microsporophylls derived,

rather than leaving polarity unspecified. The extreme fern rooting extrapolates from the fact that ferns have scalariform primary xylem pitting to the conclusion that the scalariform secondary xylem pitting of angiosperms is primitive, and from the observation that the stems of ferns look more like the manoxylic stems of cycads than the pycnoxylic stems of conifers and *Ginkgo* to the conclusion that manoxylic characters such as multiseriate rays are ancestral. These extrapolations now seem highly questionable, not only in light of the anatomy of progymnosperms and seed ferns (Beck, 1970), but also because they compare the primary xylem of ferns with the secondary xylem of seed plants. However, there is again historical precedent for considering these views; for example, the scalariform pitting of angiosperms has often been cited as an archaic feature suggesting that they were derived from some unknown primitive group of seed ferns (e.g., Takhtajan, 1969).

With both fern rootings, the most parsimonious trees included the same two derived from the conservative rooting (Fig.4.a, f). Here the course of leaf and sporophyll evolution necessarily follows the patterns shown in Fig.5.a, d. However, the extreme fern rooting yielded three additional trees in which angiosperms are basal in seed plants and Gnetales are associated with coniferopsids, varying in the arrangement of conifers and *Ginkgo* (Fig.6.a). With the conservative and moderate fern rootings, such trees are one step less parsimonious than the shortest trees. In terms of character evolution, these trees imply that the scalariform pitting, flat guard cells, and cellular embryogeny of angiosperms are all primitive features directly retained from a fern ancestry, as assumed by Takhtajan (1969) for pitting, rather than secondary reversals. The last two features were also coded as ancestral in the previous experiments, but by themselves they were not enough to shift angiosperms to a basal position.

Progymnosperm rooting

The "progymnosperm" rooting differs from all others in assuming that the simple, non-

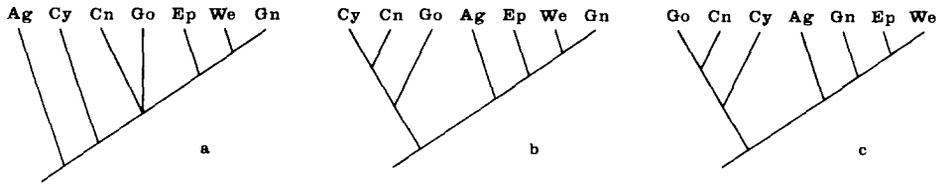


Fig.6. Additional most parsimonious trees obtained with (a) the extreme fern rooting (60 steps), (b) the progymnosperm rooting (61 steps), and (c) the seed fern rooting (58 steps). The trichotomy in (a) indicates that all three possible arrangements of the taxa concerned were found.

pinnate leaves and sporophylls of coniferopsids are primitive relative to the pinnate leaves of cycadopsids, being less removed from the dichotomous appendages of progymnosperms. Since progymnosperms have secondary wood and more uniform reproductive morphology than living outgroups, they allow uniseriate rays, circular-bordered secondary xylem pitting, free microsporangia, and radial, non-saccate (pseudosaccate) pollen with alveolar exine structure to be designated as ancestral. However, since they lack seeds, the polarity of most seed characters cannot be specified (except terminal ovules, which seem derived under any reasonable homology of ovules with progymnosperm structures). Since the stomatal structure of progymnosperms is unknown, we follow the modern data in designating raised guard cell poles as derived.

It might be thought that using progymnosperms to root extant groups would favor the concept that coniferopsids and cycadopsids are sister groups, but in fact it results in the same two trees found with the conservative and fern rootings (Fig.4.a, f) plus a new tree that places cycads within coniferopsids as the sister group of conifers, leading to the bizarre conclusion that cycads are derived from coniferopsid-like ancestors (Fig.6.b). Although two of the three trees have topologies seen with the fern rootings, they all differ radically from the fern-rooted trees in terms of character evolution. Two of them (Figs.4.f and 6.b) imply that pinnate leaves and sporophylls are independently derived from simple structures in all cases where they occur (angiosperms, cycads, *Gnetum*, as in Fig.5.e), favoring the concept

that angiosperms are derived from Gnetales-like ancestors (this is equivocal in Fig.4.a: contrast Fig.5.b, c). For the same reasons, they contrast with trees derived from the whole data set. However, they also differ from "Beck-type" trees obtained by manipulation of the whole data set, in which coniferopsids are associated with *Archaeopteris* but the topology of other groups remains unchanged. In such trees, pinnate leaves are still basic within cycadopsids and Gnetales are reduced relative to angiosperms.

Although our analysis of the whole data set assumed that seed plants are ultimately derived from *Aneurophyton*-like progymnosperms, it should not be surprising that coding ancestral states for extant groups in terms of progymnosperms gives such different (and presumably incorrect) results, since progymnosperms are more distant from modern seed plants than seed ferns are (cf. Maddison et al., 1984).

Seed fern rooting

The "seed fern" rooting is based on the assumption that the closest outgroups of the clade including all modern seed plants are *Medullosa* and lyginopterid seed ferns, as in many of the shortest trees derived from the whole data set, such as Fig.1. Like the fern rootings, this arrangement implies that pinnate leaves and sporophylls are ancestral. Like the progymnosperm rooting, it allows conclusions on the polarity of many characters that comparison with modern outgroups left undirected. It agrees with the progymnosperm rooting on the polarity of the tracheary

pitting, saccate pollen, and exine structure characters, but it differs in treating as ancestral multiseriate rays and microsynangia (apparently derived from the progymnosperm conditions in early seed ferns), raised guard cell poles, and radiospermic seeds. However, the polarity of several other characters either remains or becomes equivocal: presence vs. absence of a cupule (potentially, though probably not actually, represented today by the angiosperm outer integument), uni- vs. multilacunar nodes, and radial vs. bilateral pollen; in each case, the former state occurs in lyginopterids, the latter in *Medullosa*. As noted above, the large size of the egg cell suggests that seed ferns had free-nuclear embryogeny, but to be cautious we left this character unpolarized.

If the correct outgroups are sufficient to establish correct ingroup relationships even when the ingroup is incomplete, this rooting should give the trees most consistent with those obtained from the whole data set. Quite to the contrary, for the first time both topologies of extant groups derived from the whole data set (Fig.4.a, b) are eliminated: they are now one or two steps longer than the shortest trees, which are the tree with cycads linked with coniferopsids (Fig.4.f) and a new tree with *Gnetum* basal in Gnetales (Fig.6.c).

With this rooting, user-specified trees with angiosperms basal (Fig.4.e) become three steps less parsimonious than the shortest trees, implying that knowledge of early seed ferns should have eliminated the idea that the scalariform pitting and other fern-like features of angiosperms are primitive retentions. This effect is even more striking with the progymnosperm rooting, where the difference is six steps.

Despite the different placement of cycads, the trees obtained with the seed fern rooting are certainly closest to those derived from the whole data set in terms of inferred pathways of character evolution leading to coniferopsids, angiosperms, and Gnetales (and presumably adaptive scenarios for their origin). Thus with the topology in Fig.4.f, changes in leaves and sporophylls follow the pattern in Fig.5.d, and

pycnoxylic anatomy is derived from manoxylic. However, without additional information from ingroup fossils such as Mesozoic seed ferns and Bennettitales, the inferred homologies of the angiosperm outer integument and most of the course of pollen evolution would still be obscure.

Since all of our experiments produced one or more trees with coniferopsids nested in seed plants, and since it is most parsimonious to assume that the seed arose only once even when coniferopsids are basal, one may ask why historically the idea of diphyletic origin of seed plants flourished before as well as after the recognition of progymnosperms (e.g., Chamberlain, 1935; Arnold, 1948). One reason may be that evidence amassed by Florin (1938–1945, 1951) suggested that the leaves and sporophylls of Paleozoic conifers and cordaites are basically dichotomous, and this was assumed to be a retention of the primitive dichotomous organization of Devonian vascular plants, which lacked seeds. A logical alternative, that both coniferopsids and cycadopsids were derived from a coniferopsid-like common ancestor with dichotomous leaves and seeds, was not considered, perhaps because seed ferns were assumed to be derived from ferns, and/or because they appear stratigraphically before coniferopsids. Some might cite this as a case where overreliance on fossils obscured true relationships (cf. Patterson, 1981). However, it might be better attributed to a tendency to assume that evolution of certain characters is irreversible, an error independent of the question of the value of fossil evidence. Furthermore, it is far from clear that the concept of a diphyletic origin of the seed is incorrect, since it is almost as parsimonious when the whole data set is analyzed (Doyle and Donoghue, 1986).

In summary, the experiments described so far show that parsimony analysis of extant ingroups and outgroups only does produce one topology of seed plant taxa (among several others) that is identical to one of the two derived from analysis of both living and fossil groups, but even with this "correct" topology implications on character evolution and adap-

tive scenarios for the origin of major groups are very poorly constrained. Addition of appropriate fossil outgroups (early seed ferns) clarifies many problems of character evolution, but it leaves others unresolved (e.g., evolution of the angiosperm outer integument), and ironically it does not give either of the topologies seen in analysis of the whole data set.

These observations indicate that fossils are important in providing not only closer outgroups but also new members of the ingroup. The remaining experiments address the role of fossil ingroup taxa by adding selected fossils to the modern data set or subtracting them from the whole data set. The addition experiments were done with both the conservative rooting and the seed fern rooting, corresponding to hypothetical situations where (1) only modern groups and the added fossil ingroup taxa are known, and (2) both the added ingroup taxa and primitive Carboniferous seed ferns are known.

Archaeopteris, Callistophyton, and the position of coniferopsids

Based on the notion that it is the coniferopsid features of *Archaeopteris* that most strongly suggest a separate origin of coniferopsids and cycadopsids from progymnosperms (Beck, 1970), and the fact that it was recognition of coniferopsid characters in *Callistophyton* that led to the alternative hypothesis that coniferopsids were derived from platyspermic seed ferns (Rothwell, 1982), we performed a set of experiments subtracting *Archaeopteris*, *Callistophyton*, and *Callistophyton* plus other platyspermic seed fern groups from the whole data set and adding *Callistophyton* to the extant data set. No characters are lost with subtraction of *Callistophyton* from the whole data set, but subtraction of *Archaeopteris* entails loss of characters 3 and 32; as explained above, without reference to *Archaeopteris* these are not obvious as synapomorphies of coniferopsids. When all platyspermic seed ferns are removed, the bifurcate vs. simple rachis character is lost, since there are no longer any

groups with pinnately compound leaves and a simple rachis; flat guard cells become an angiosperm autapomorphy; and the distinctions among the various sorts of bitegmic and cupulate ovules (lyginopterids, angiosperms, Bennettitales and *Pentoxylon*) become problematical, so we collapsed multistate character 33–34 to a binary character, with cupules ancestral. Addition of *Callistophyton* to the modern data set (Table V) required reinstatement of the distinctions between mesarch and endarch primary xylem and between pinnately compound and once-pinnate leaves and sporophylls (simplified to 00 and 10, respectively). In the whole data set we scored coniferopsid leaves X01, one step from either progymnosperms or seed ferns but two steps from once-pinnate groups (e.g., cycads), since there are no current hypotheses that propose that they are derived from once-pinnate ancestors; however, with the present limited data set, there would be no grounds for biasing against any sort of ancestry, so we rescored them X1 (for XX1).

As expected, when *Archaeopteris* is removed from the whole data set, trees with coniferopsids forced into a sister-group relationship with cycadopsids, as under the Beck hypothesis, became three steps less parsimonious (121 steps) than trees with coniferopsids nested in seed plants (118 steps); in both cases, the topology of other groups was unaffected (cf. Fig. 1). This is actually an underestimate of the difference in parsimony between the two current hypotheses on the origin of coniferopsids, since the artificial topology with coniferopsids directly below lyginopterids is not a perfect model of the Beck hypothesis in terms of character evolution. With this topology, the Wagner algorithm assumes that the seed and axillary branching are homologous in coniferopsids and cycadopsids, whereas under the Beck hypothesis they arise twice. This implies that without *Archaeopteris* there would be little basis for believing that coniferopsids and cycadopsids originated separately from progymnosperms.

When *Callistophyton* was removed from the

TABLE V

Experiments with addition of fossils to extant taxa. "Conservative" and "seed fern" designate sets of user-specified ancestral states based on different assumptions concerning outgroup relationships. "BGAS" represents "best guesses" of ancestral states provided by PHYLIP for selected most parsimonious trees obtained with the conservative rooting

Adding **Callistophyton**:

	1	2	3	4	5	6
Conservative	-0-0-0X-0-100--X000X0XX0-0X-0XX--XX-XXX0-X--XXX--XXXXX-0000010					
Seed fern	-0-0-00-0-000--0X00001X0-00-000--X0-0100-0--0XX--XX000-00000X0					
Callistophyton	-0-0-00-0-X0X--00000010X-00-000--00-110X-1--00X--01100-00XX0XX					
BGAS, tree 7c:	-0-0-00-0-100--X00000100-00-000--00-1100-1--000--01X00-0000010					

Adding Bennettitales (ancestral states specified as with extant taxa):

	1	2	3	4	5	6
Bennettitales	-0-0--0-0-01X---0001011X--1--00--10-0110-X--10X--01010-1XX00XX					
BGAS, tree 8a:	-0-0--0-0-100---000X01X0--X--00--X0-XX00-1--000--010X0-0000010					
BGAS, tree 8d:	-0-0--X-0-100---00000XX0--X--X0--00-1000-1--000--01000-0000010					

Adding **Caytonia** and Bennettitales:

	1	2	3	4	5	6
Conservative	-0-0-0X-00100---000X0XX0--X-0XX--XX-XXX0-X--XXX--XXXXX-0000010					
Seed fern	-0-0-00-000000---X00001X0--0-000--X0-0100-0--0XX--XX000-00000X0					
Caytonia	-0-0-00-1010X---XXXXXXXXX--0-000--10-X10X-1--001--01100-1XXXXXX					
Bennettitales	-0-0-10-0001X---0001011X--1-100--10-0110-X--10X--01010-1XX00XX					
BGAS, tree 9a:	-0-0-00-00100---000X01X0--0-000--X0-1X00-1--00X--01000-0000010					
BGAS, tree 9c:	-0-0-0X-00100---00000XX0--X-0X0--00-1000-1--000--01000-0000010					
BGAS, tree 9f:	-0-0-00-00100---000X01X0--0-000--X0-XX00-1--00X--01000-0000010					

whole data set, we obtained one tree with coniferopsids linked to *Archaeopteris* (Fig.7.a) that is just as parsimonious (121 steps) as any with coniferopsids nested in seed plants (in the latter, other groups may be arranged as in either Fig.7.a or Fig.1). It might be surmised that the shift in favor of the Beck hypothesis is not greater than this because the presence of other platyspermic seed ferns compensates in part for removal of *Callistophyton*. To some extent, this appears to be true: when the remaining platyspermic, saccate groups and *Peltaspermum* are also removed, it becomes more parsimonious to link coniferopsids with *Archaeopteris* than to nest them in seed plants (Fig.7.b), but only by one step (96 vs. 97). Interestingly, however, knowledge of such

groups appears to be needed for "correct" placement of the coniferopsids, since in Fig.7.b coniferopsids move below *Medullosa*.

In summary, these experiments indicate that knowledge of *Archaeopteris* is more important for the Beck hypothesis that coniferopsids and cycadopsids were independently derived from progymnosperms than knowledge of *Callistophyton* is for the Rothwell hypothesis that coniferopsids originated from platyspermic seed ferns. This is partly because of the existence of other platyspermic seed ferns, but even if such groups were unknown, both hypotheses would still be viable. Presumably the reason that these forms were not recognized as evidence for a seed fern origin of coniferopsids is that they are all considerably

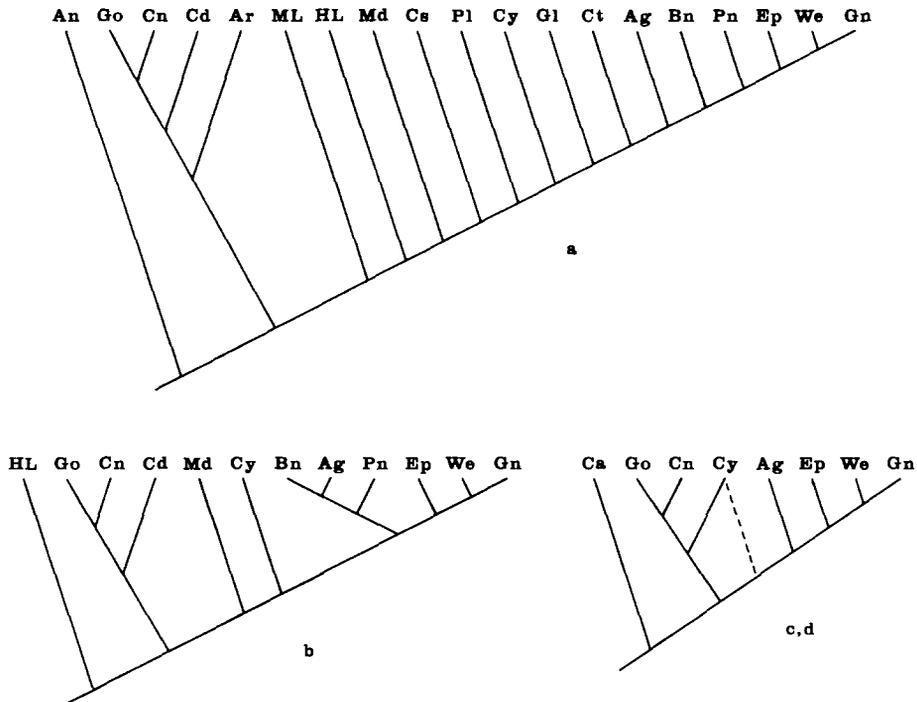


Fig.7. Experiments with *Archaeopteris* and *Callistophyton*. (a) Most parsimonious tree obtained after subtraction of *Callistophyton* (121 steps). (b) Tree obtained after subtraction of all platyspermic seed ferns (97 steps); this is one step less parsimonious than the shortest tree found, which linked coniferopsids with *Archaeopteris* (taxa not shown arranged as in Fig.1). (c, d) Most parsimonious trees obtained after addition of *Callistophyton* to extant taxa (c and d differ in that cycads are placed as shown by the solid and dashed lines, respectively); with the conservative rooting only tree (c) was found (64 steps), but with the seed fern rooting both trees were found (65 steps).

younger than the first coniferopsids, so they seemed less relevant to the problem than a Carboniferous fossil with similar features.

Experiments with addition of *Callistophyton* to the modern data set show that knowledge of this genus does not markedly affect relationships of extant groups, but it does improve inferences on character evolution. In both trees obtained (Fig.7.c, d), *Callistophyton* is basal, consistent with several most parsimonious trees based on the whole data set (though not Fig.1). This arrangement is supported by the fact that all extant groups are endarch, whereas *Callistophyton* is mesarch or exarch. Addition of *Callistophyton* corrects an anomaly noted above, namely that the arrangement of extant groups seen in Fig.1 and many other trees derived from the whole data set (i.e., Fig.4.a) was not seen when lyginopterid seed

ferns and *Medullosa* were used to root extant groups, even though these are presumably the most appropriate outgroups. The one tree found with the conservative rooting links coniferopsids with cycads (Fig.7.c), but with the seed fern rooting the topology seen in Fig.1 also appears (Fig.7.d). Turning to character evolution (cf. BGAS, Table V), even with the conservative rooting it becomes most parsimonious to assume that coniferopsids originated from ancestors with pinnate leaves, as inferred from the whole data set. With the seed fern rooting, even though radiospermic was specified as ancestral, it is more parsimonious to assume that platyspermic seeds arose before the immediate common ancestor of extant groups and *Callistophyton* and secondarily reverted to radiospermic in cycads and *Gnetum* (as in Fig.1) than to assume that platyspermic

originated several times. However, it is still most parsimonious to assume that saccate pollen arose independently in *Callistophyton* and conifers.

For symmetry with our experiments with the seed fern and progymnosperm rootings of the modern data set, it might be interesting to observe effects of subtracting Carboniferous seed ferns from the whole data set but leaving in progymnosperms. However, we did not carry out such an exercise, since we found that the problems of character analysis soon become intractable, especially in the multistate characters (e.g., cupules, radio- vs. platyspermic seeds, stelar types), for which ideas on the ancestral condition and the interrelationships of derived states depend heavily on knowledge of early seed ferns. This is itself a measure of their importance in understanding the evolution of extant groups.

Bennettitales, Caytonia, and relationships of angiosperms and Gnetales

Another case where fossils appear to provide important links among extant taxa concerns the relationship of angiosperms and Gnetales to each other and to other groups. Although our analysis of extant taxa links Gnetales with angiosperms, trees in which Gnetales are nested within coniferopsids are only one step longer (Fig.4.e). Without parsimony analysis, angiosperm–gnetalian relationships are easy to dismiss (e.g., Doyle, 1978) because of the many coniferopsid features of Gnetales (wood anatomy, compound strobili), the great morphological gap between angiosperm and gnetalian reproductive structures, and the fact that many of the most striking similarities between angiosperms and Gnetales (e.g., the dicot-like leaves of *Gnetum*, possibly vessels) appear to be primitively lacking in some members of one or the other group. Other angiosperm–gnetalian similarities remain, but they tend to be rather cryptic (e.g., the tunica layer in the apical meristem, Mäule reaction, siphonogamy, granular exine structure). Our analysis of the whole data set suggests that

Bennettitales play a key role in strengthening the angiosperm–gnetalian connection. Specifically, more features of Gnetales are accounted for if they are considered highly modified relatives of Bennettitales rather than coniferopsids (e.g., syndetocheilic stomata, whorled microsporophylls, micropylar tube); and Bennettitales help to link Gnetales with angiosperms, since they have several angiosperm-like traits that are lacking in Gnetales, apparently because of secondary loss (e.g., scalariform pitting, cupulate ovules). Likewise, as pointed out by Crane (1985), Mesozoic seed ferns (*Caytonia*, corystosperms, and/or glossopterids) appear to link the resulting “anthophyte” clade with other seed plants, thus reconciling ideas of a relationship between angiosperms and Mesozoic seed ferns (Gaussen, 1946; Stebbins, 1974; Doyle, 1978) and among angiosperms, Bennettitales, and Gnetales. For example, *Caytonia*, corystosperms, and anthophytes have a reduced megaspore wall; *Caytonia*, glossopterids, angiosperms, most Bennettitales, and *Pentoxylon* have a thick nucellar cuticle; and Bennettitales and *Pentoxylon* have an orthotropous cupule that might correspond to the anatropous cupule of *Caytonia* and/or corystosperms and the outer integument of angiosperms.

To explore the effects of Bennettitales on relationships of angiosperms and Gnetales, we performed two sets of experiments: adding Bennettitales to the modern data set and subtracting Bennettitales and *Pentoxylon* (which have many of the same features and hence might be expected to produce similar results independently) from the whole data set. No new characters appear with addition of Bennettitales. Both anatropous and orthotropous cupulate ovules now occur, but we combined them and left the ancestral state unspecified, since their relations to each other and to other states would be obscure. Without knowledge of the leaflet-like anatropous cupules of *Caytonia* and corystosperms or the evidence that these taxa are nested among groups with non-cupulate, laminar ovules, there would be less reason to suspect that there

are two sorts of cupules in seed plants: the radial lyginopterid type that appears to be basic in seed plants, and an unrelated type secondarily derived from an enrolled ovule-bearing leaflet. Similarly, no characters are lost when Bennettiales and *Pentoxylon* are subtracted.

As expected, these experiments show that knowledge of Bennettiales does strengthen relationships between angiosperms and Gnetales. When Bennettiales are added to the modern data set (Fig.8.a-e), the three angiosperm groups are always associated. With the conservative rooting all possible arrangements of the three groups are found (Fig.8.a-e), but with the seed fern rooting (i.e., better outgroup information) Bennettiales are linked with Gnetales (Fig.8.a), as inferred from the whole data set. With Bennettiales present, moving Gnetales into the coniferopsids (Fig.8.f) adds two or three steps (depending on the rooting), whereas with the modern data set one tree with Gnetales nested in coniferopsids (Fig.4.e) was only one step longer than the shortest trees. When Bennettiales and *Pentoxylon* are subtracted from the whole data set, trees with

Gnetales nested in coniferopsids are only one step less parsimonious than trees where they are linked with angiosperms (115 vs. 114 steps), rather than four steps less parsimonious. Arrangements of other groups are not affected (cf. Fig.1); thus when Gnetales are moved into coniferopsids, angiosperms remain linked with *Caytonia*, as previously assumed by one of us (Doyle, 1978) after overlooking or rejecting as convergences the angiosperm and gnetalian features of Bennettiales.

Knowledge of Bennettiales also has some effect on inferred character evolution in angiosperms and seed plants as a whole (BGAS, Table V). For example, two of the five shortest trees obtained with the conservative rooting (Fig.8.a, b) imply that pinnate leaves are ancestral in seed plants and that the linear leaves and simple microsporophylls of Gnetales and coniferopsids are independently reduced, as inferred from the whole data set. In contrast, the course of evolution in these characters is equivocal in all trees of extant taxa alone based on the same rooting. If it is assumed that vessels are basic in angiosperms, analysis of modern groups alone would imply

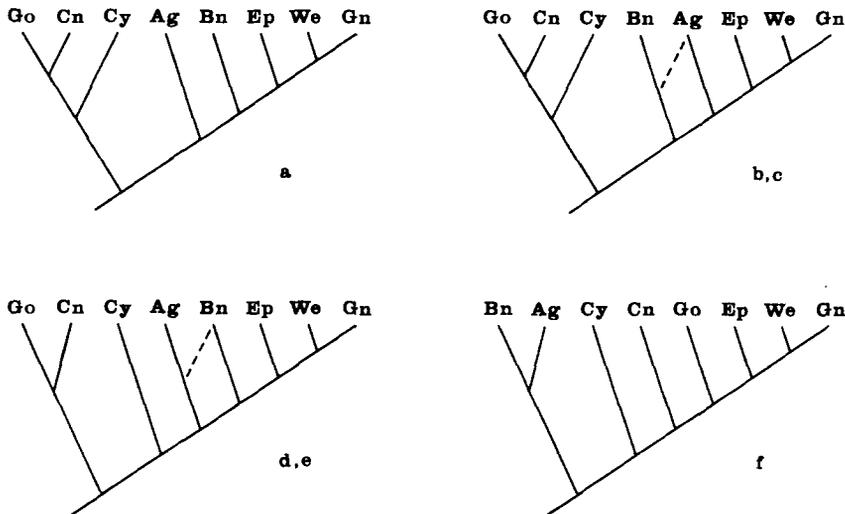


Fig.8. Experiments with addition of Bennettiales to extant taxa (b and d differ from c and e in that the groups indicated are placed as shown by the solid and dashed lines, respectively). With the conservative rooting, five most parsimonious trees were found (a-e, 63 steps), while with the seed fern rooting only tree (a) was found (62 steps). (f) Tree with Gnetales forced into coniferopsids (66 steps with the conservative rooting, 64 steps with the seed fern rooting).

that vessels are homologous in angiosperms and Gnetales, but in trees with Bennettitales added (except Fig.8.b) it becomes equally parsimonious to assume that they originated independently. However, four of the five trees (Fig.8.b–e) imply that the stalked or sessile ovules of coniferopsids, Bennettitales, and Gnetales are primitive, whereas our analysis of the whole data set indicates that they were derived by reduction.

To probe the importance of *Caytonia* and possibly related forms in elucidating the position and character evolution of the angiosperms, we added *Caytonia* to the modern data set and subtracted *Caytonia* and *Caytonia* plus glossopterids and corystosperms from the whole data set. In the addition experiments we reinstated the distinction between pinnately compound and once-pinnate leaves and microsporophylls (since leaflets of *Caytonia* have midribs), and between reticulate venation and presence of several vein orders. In the subtraction experiments, we eliminated flat guard cells when we subtracted *Caytonia*, plus one ovule per cupule when we subtracted all three groups; with these subtractions, these features become angiosperm autapomorphies. When all three groups were subtracted, we simplified the

cupule character and recoded Bennettitales, *Pentoxylon*, and angiosperms as having the lyginopterid state, for the same reasons discussed in connection with experiments where we added Bennettitales.

With both rootings, when *Caytonia* is added to the modern groups, it is always linked directly with angiosperms, rather than being the sister group of angiosperms plus Gnetales, and it is equally parsimonious to associate Gnetales with angiosperms plus *Caytonia* (Fig.9.b, c) or with coniferopsids (Fig.9.a, d). For comparison, trees derived from the whole data set with *Caytonia* linked with angiosperms and with Gnetales nested in coniferopsids are one and four steps less parsimonious than the best arrangements, respectively. These results again confirm the importance of Bennettitales as a link between angiosperms and Gnetales and the idea that if Bennettitales were unknown (or overlooked), the clearest relationships of angiosperms would be with Mesozoic seed ferns.

As occurred when Bennettitales were added to modern groups, when *Caytonia* is added it becomes most parsimonious to assume that pinnately compound leaves and sporophylls were basic in seed plants even in some of the

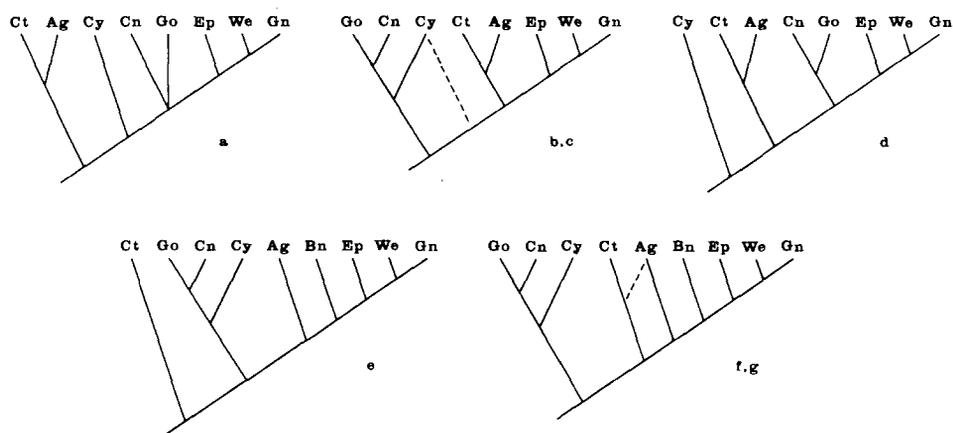


Fig.9. Experiments with addition of *Caytonia* and Bennettitales to extant taxa (b and f differ from c and g in that the groups indicated are placed as shown by the solid and dashed lines, respectively). (a–d) Trees obtained after addition of *Caytonia* alone; with the conservative rooting trees (a–c) were found (66 steps), while with the seed fern rooting trees (b) and (d) were found (65 steps). (e–g) Trees obtained after addition of both *Caytonia* and Bennettitales; with the conservative rooting trees (e) and (f) were found (71 steps), while with the seed fern rooting all three trees were found (71 steps).

trees obtained with the conservative rooting, namely those where Gnetales are nested in the coniferopsids (Fig.9.a; BGAS, Table V). However, both the basic state in seed plants and the direction of evolution within the anthophytes are still equivocal in trees where Gnetales are linked with angiosperms and *Caytonia* (Fig.9.b, c; BGAS, Table V). In the tree with Gnetales linked with angiosperms and *Caytonia* obtained with the seed fern rooting (Fig.9.b), it is most parsimonious to assume that gnetalian flowers are reduced rather than primitively simple. However, not even Fig.9.b gives a wholly satisfactory picture of character evolution in anthophytes: the angiosperm outer integument can be homologized with the *Caytonia* cupule, but it is best interpreted as a synapomorphy of *Caytonia* and angiosperms that never existed in the ancestry of Gnetales, rather than a basic feature of the whole *Caytonia*-anthophyte clade that was lost in Gnetales. Similarly, unless it is assumed that *Caytonia* once had flowers and then lost them, all these trees imply that flower-like reproductive structures originated independently in angiosperms and Gnetales, whereas they are best interpreted as homologous in the shortest trees derived from the whole data set.

This interpretation is confirmed by experiments where both Bennettitales and *Caytonia* are added to the modern taxa (Fig.9.e–g). With both rootings, trees with Gnetales associated with coniferopsids are again eliminated, but a curious new topology appears, with *Caytonia* basal in seed plants (Fig.9.e). One of the remaining trees (Fig.9.g) still links angiosperms directly with *Caytonia*, but the other (Fig.9.f) interpolates angiosperms between *Caytonia* and Bennettitales, which is the result obtained from the whole data set (Fig.1). *Caytonia* and angiosperms have two potential synapomorphies that tend to favor a close relationship (flat guard cells, reticulate venation), but when Bennettitales are present these are balanced by anthophyte features seen in Bennettitales but not *Caytonia* (once-pinnate leaves, syndetocheilic stomata, granular non-saccate pollen). Other potential anthophyte

synapomorphies such as scalariform pitting, Mäule reaction, and siphonogamy have no effect either way because the condition in *Caytonia* and/or Bennettitales is unknown. In the absence of Bennettitales, Gnetales are unable to dissociate angiosperms and *Caytonia*, apparently because several basic anthophyte features seen in angiosperms and Bennettitales (syndetocheilic stomata, cupules) are lacking in some or all Gnetales (probably due to secondary loss).

Even with the conservative rooting, addition of both Bennettitales and *Caytonia* finally allows many of the same conclusions regarding character evolution that were drawn from analysis of the whole data set (BGAS, Table V). Thus it is most parsimonious to assume that the first seed plants had seed fern-like anatomy and pinnate leaves and sporophylls, and that Gnetales originated by reduction of Bennettitales-like ancestors. Most trees (except Fig.9.g) imply that flowers are homologous in anthophytes and that the *Caytonia*-anthophyte cupule was lost in Gnetales. However, the origin of the cupule remains obscure; without information on more primitive seed ferns, it is equivocal whether it is homologous with the original lyginopterid cupule or a secondary innovation (as inferred from the whole data set).

The subtraction experiments suggest that if *Caytonia* and potentially related forms were unknown there would be little support for derivation of anthophytes from seed ferns with platyspermic seeds and saccate pollen. When *Caytonia* alone is removed, two most parsimonious positions for the anthophytes are found, linked with corystosperms or with glossopterids (119 steps, with various arrangements of other groups). This is not surprising considering that glossopterids are the next-closest relatives of anthophytes in all 123-step trees derived from the whole data set (e.g., Fig.1), while corystosperms are their closest relatives in some 124-step trees. When *Caytonia*, corystosperms, and glossopterids are removed, the best position for anthophytes is linked with cycads and *Peltaspermum* (Fig.10.a, b). This

topology is consistent with that derived from the whole data set, but although it implies that anthophytes are basically platyspermic, it suggests that they never had ancestors with saccate pollen. In fact, with removal of so many saccate groups, it becomes most parsimonious (by one step) to rearrange coniferopsid taxa so that ginkgos are basal and to assume that saccate pollen originated independently in *Callistophyton* and within coniferopsids, rather than being basic for the whole platyspermic clade. Another conflict with trees based on the whole data set is that Gnetales are the sister group of angiosperms, Bennettitales, and *Pentoxylon*; with removal of outgroups with potentially homologous cupules, it is most parsimonious to assume that the cupule (outer integument) of Bennettitales, *Pentoxylon*, and angiosperms is an innovation of those groups that never existed in the ancestry of Gnetales.

Interestingly, angiosperms seem to play the same role in linking Bennettitales and Gnetales with Mesozoic seed ferns that Bennetti-

tales play in linking angiosperms with Gnetales. When angiosperms are subtracted from the whole data set, the shortest tree found (113 steps) is of the neo-englerian type, with Bennettitales, *Pentoxylon*, and Gnetales nested in coniferopsids (Fig.10.c). This arrangement suggests that the flowers of Bennettitales are secondarily elaborated from coniferopsid axillary fertile shoots via gnetalian intermediates. With the whole data set, such trees are two steps longer than the shortest trees (and highly implausible on developmental grounds) because of the numerous secondary elaborations and de novo origins of seed fern-like features that must be assumed in angiosperms and/or Bennettitales (pinnate leaves and microsporophylls, multiseriate rays, scalariform primary xylem, cupules, microsynangia). However, since Bennettitales and *Pentoxylon* are more coniferopsid-like than angiosperms in having stalked or sessile ovules, there are fewer steps to reverse when angiosperms are ignored. Basically, the presence of pinnately organized

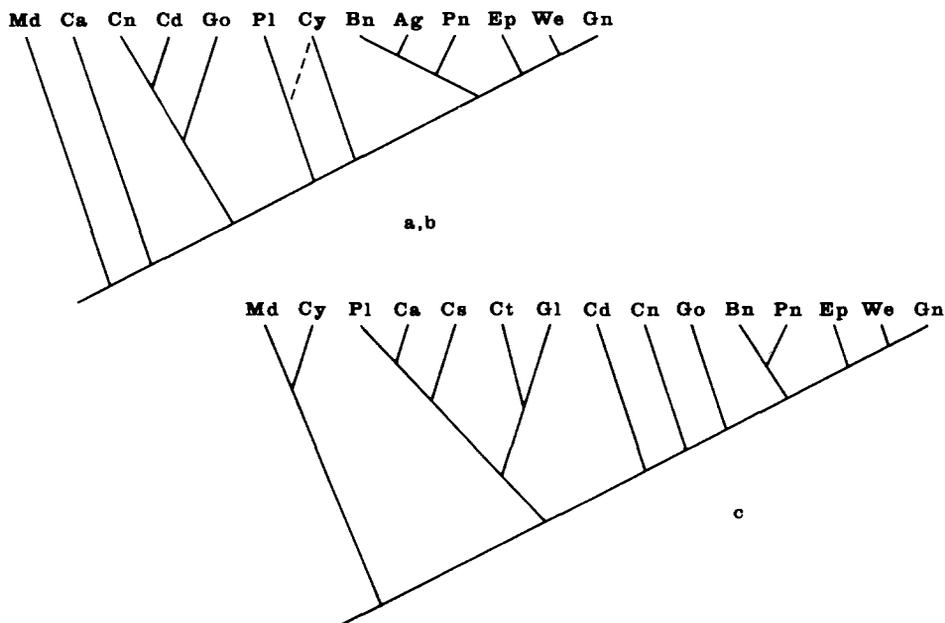


Fig.10. Experiments with subtraction of Mesozoic seed ferns and angiosperms (groups not shown arranged as in Fig.1). (a, b) Most parsimonious trees obtained after subtraction of *Caytonia*, glossopterids, and corystosperms (104 steps; a and b differ in that cycads are placed as shown by the solid and dashed lines, respectively). (c) Most parsimonious tree obtained after subtraction of angiosperms (113 steps).

carpels and anatropous bitegmic ovules in angiosperms shifts the balance to the scheme derived from the whole data set. This illustrates graphically the point that although fossils may be useful or even necessary in understanding the origin and relationships of living groups, living groups have a similar role in understanding the relationships of fossils (cf. Hennig, 1966).

General implications

In general, our results lead us to a more positive view of the value of fossils in phylogeny reconstruction than that of Patterson (1981) — in many respects, a return to the generalizations of Hennig (1966) summarized in the introduction. We agree that the primary way that fossils provide phylogenetic information is just as additional extant groups do, namely by providing new character combinations that may necessitate changes in cladogram topology. However, Patterson's empirical claim that this rarely occurs in practice seems overstated. The study of Gauthier, Kluge and Roe (pers. commun., 1985) on amniotes shows that fossils can dramatically alter conclusions on relationships. Our results do not contradict Patterson's conclusions so directly, since cladogram topologies derived from extant taxa alone are either similar or identical to topologies derived from our whole data set. However, our study focuses attention on a more subtle but equally important point, which we believe has received less consideration than it deserves: even when fossils do not change cladogram topologies, they may greatly clarify and in some cases reverse ideas on the nature and sequence of character changes involved in the origin of major groups. This may provide otherwise quite inaccessible insights into evolutionary processes involved, especially when combined with other sorts of information provided by the geologic record.

Closer examination of our results from a theoretical viewpoint may allow more detailed generalizations on ways that fossils can change phylogenetic conclusions, and this may

help identify cases where fossil evidence is more or less likely to be important in the future. These questions were also addressed by Fortey and Jeffries (1982), who concluded that fossils are most likely to be significant when there has been homoplasy in characters of high "burden" that characterize major groups (i.e., characters on whose presence the existence of other characters depends). Since complete loss of such characters is unlikely, Fortey and Jeffries suggest that fossils will seldom change topological relationships of extant groups, but when they do the effects may be profound because of the rank of the taxa involved. While we find this concept intriguing and worth further exploration, we would propose a somewhat different set of generalizations, based on our present results and the analysis of Maddison et al. (1984), who have considered the general effects of adding information on new groups to cladistic analysis. We expect that fossils are most likely to lead to changes in topology when (1) the ingroup is separated from the outgroup by large gaps, i.e., numbers of steps (as extant seed plants are separated from extant "pteridophytes"); (2) there are major gaps in the ingroup (as between angiosperms, Gnetales, and other seed plants); and (3) there is evidence of homoplasy, so that alternative placements of groups (e.g., of Gnetales with angiosperms and coniferopsids) are almost equally parsimonious. Topological changes are especially likely when more than one of these conditions hold. Conversely, when gaps between extant groups are small (as in many angiosperm families), or there are few character conflicts, fossils are less likely to have major effects.

In the present study, despite the large gaps between extant seed plants and other groups and between angiosperms and Gnetales, fossil data did not overturn relationships inferred from extant groups alone, but they did affect the stability of relationships. Thus knowledge of Bennettitales greatly strengthens the link between angiosperms and Gnetales, which is otherwise only slightly more parsimonious than a link between Gnetales and coniferop-

sids. With a slightly different choice of characters, the relative parsimony of the two arrangements could easily have been reversed. In this context, it is worth noting that our approach may have been overly optimistic in modeling how well a hypothetical student of extant groups would analyze characters. We derived our extant data set from one based on both living and fossil groups, where character interpretations were strongly influenced by knowledge of fossils, and although we tried to reformulate all characters as a hypothetical student of extant groups might do, a real investigator would probably have interpreted some characters in unexpected ways. Perhaps a more realistic model is provided by comparison of the cladistic analyses of seed plants presented by Hill and Crane (1982), who considered extant groups only, and by Crane (1985), who included fossils as well. Hill and Crane's favored cladogram differs from all those discussed so far in treating angiosperms as the sister group of conifers plus Gnetales, and cycads plus *Ginkgo* as the sister group of the resulting clade. This result was not supported by a numerical parsimony analysis of Hill and Crane's data (Doyle and Donoghue, 1986), but the tree that we obtained from their data still differed from trees derived from our whole data set (angiosperms were the sister group of either Gnetales or *Gnetum*, and angiosperms and Gnetales were nested within coniferopsids, a neo-englerian arrangement). In contrast, as discussed above, Crane's (1985) scheme is much closer to ours in most respects, including not only the relationship of angiosperms, Bennettiales, Gnetales, and Mesozoic seed ferns, but also the arrangement of extant groups. Another more realistic example of results obtained from consideration of extant groups alone is provided by the scheme of Bremer (1985), who linked seed plants with ferns on pinnate leaves and trichomes, features that fossil evidence indicates arose independently.

Looking ahead, major gaps remain at several places in the phylogeny of seed plants even when fossils are included, and homoplasy is clearly widespread. In particular, anthophytes

are still separated from Mesozoic seed ferns by several steps, and both angiosperms and Gnetales are isolated from other anthophytes by numerous pomorphies (at least 12 in each case: Doyle and Donoghue, 1986). Thus it should not be surprising if future discoveries of fossils with unexpected character combinations alter inferred relationships. For example, discovery of fossils below the anthophyte node might modify connections between anthophytes and other groups and relationships among anthophytes. Likewise, recognition of closer fossil relatives of the angiosperms might force reevaluation of basic angiosperm states and favor direct association of angiosperms with Bennettiales or Gnetales (cf. Crane, 1985; Doyle and Donoghue, 1986).

Our results provide many illustrations of the point that even when fossils have no effect on cladogram topology, ideas on the evolution of characters based on extant groups alone may be nebulous or even incorrect, and addition of appropriate fossils may eliminate many alternatives. Thus with extant groups only, the direction of leaf evolution in seed plants is entirely ambiguous. However, when information from closer fossil outgroups is added (lyginopterid seed ferns and *Medullosa*, or *Callistophyton*), it becomes most parsimonious to assume that the first seed plants had pinnately compound leaves, and that there was a double trend from a "cycadopsid" to a "coniferopsid" habit and linear-dichotomous leaves in coniferopsids and Gnetales. The same is true when appropriate ingroup taxa are added (Bennettiales, *Caytonia*, especially both). Without fossils, the direction of floral evolution in the anthophytes is also ambiguous, but when seed ferns or *Caytonia* plus Bennettiales are added, the balance shifts to the interpretation that gnetalian reproductive structures are reduced and aggregated relative to flowers of angiosperms and Bennettiales (Arber and Parkin, 1907, 1908), rather than primitively simple (Von Wettstein, 1907). Similarly, without Mesozoic seed ferns such as *Caytonia* there is little indication of where structures such as the carpel or the outer

integument came from. Without fossil data, saccate pollen would appear to be a conifer autapomorphy, rather than a basic feature of the ancestors of all modern seed plants that was lost several times. Likewise, without plesiomorphic vesselless groups of angiosperms (Bennettitales, *Pentoxylon*) vessels could be considered homologous in angiosperms and Gnetales, but with Bennettitales and *Pentoxylon* included in the analysis it is clear that they arose independently.

All the points made so far apply equally to addition of any newly discovered taxa, which leads us to ask what if anything is "special" about fossils. Obviously, stratigraphic distribution is such a special element, but we would argue that fossils provide unique insights even if stratigraphy is ignored, as it was in our analysis. This is not because of any intrinsic properties of fossils but rather because of the way evolution seems often to proceed. As was recognized by Hennig (1969), Jeffries (1979), and Patterson (1981) in elaborating the concept of "stem groups" and "crown groups", most of the extant biota consists of large clades (e.g., mammals, birds, angiosperms) that are separated from their closest extant relatives by major gaps (large numbers of apomorphies). Plesiomorphic fossil relatives of these crown groups (members of their stem groups, which are by definition paraphyletic) often show that apomorphies were acquired in a stepwise fashion, culminating in the complex of advances seen in the crown group. Patterson (1977, 1981) gives an excellent example of this phenomenon in the origin of teleost fishes. This pattern might be suspected without fossils, but the actual sequence of origin of apomorphies would be entirely speculative. Hennig (1966) argued that such information may alter ideas on relationships of extant taxa, and this expectation is confirmed by the work of Gauthier et al. (pers. comm., 1985) on amniotes. Relationships among seed plant taxa seem to be less affected, but the Devonian progymnosperms and Carboniferous seed ferns making up the stem group document in great detail the sequential acquisition of secondary growth,

pinnately compound leaves, axillary branching, the seed, and the eustele, modernization of the ovule and pollen-capture system, and origin of saccate pollen, basic features of the crown group to which all extant seed plants belong. Similarly, Mesozoic seed ferns and Bennettitales fill in steps in the origin of angiosperms, such as appearance of scalariform secondary xylem pitting, derivation of the outer integument from a reflexed leaflet and the carpel from a sporophyll rachis, loss of air sacs in the pollen, and a shift to granular exine structure. Bennettitales show steps leading to Gnetales, such as reduction of the megasporophylls, whorling of the microsporophylls, and origin of a micropylar tube. Judging from extant data alone, the gaps between crown groups could conceivably be due solely to anagenesis in single stem species, but since stem group taxa often consist of numerous coexisting species (e.g., lyginopterids, medullosans), only one of which can be directly ancestral to the crown group, it is more likely that the origin of gaps involved extensive cladogenesis followed by extinction, whether due to displacement of older "experimental models" by the crown group as a result of a superior combination of features or to stochastic effects.

Given the present state of exploration of the earth's biota, it is highly unlikely that the gaps between crown groups will be filled by discoveries of rare extant taxa. Instead, this will be accomplished primarily by discovery of new fossils, or since Meyen (1984) may be correct in believing that most major land plant groups are already known at least as isolated organs, by reconstruction of new groups from their component parts (as illustrated by *Archaeopteris* and *Callistophyton*). Here it is worth noting that although plants are notorious for being preserved as isolated organs, which are difficult to fit into phylogenetic analysis (cf. Hennig, 1966), plant cells have more or less resistant walls, so that more organ systems are potentially fossilized than in animals (especially in the Paleozoic, thanks to the unusual anatomical preservation seen in coal balls). In fact, at least some members of many major

fossil groups have been reconstructed almost as completely as modern plants. This suggests that the possibilities of gaining phylogenetic information from fossils are as good or better in plants than in animals, at least at higher taxonomic levels.

The greater resolution of character evolution provided by fossils is relevant not only to relationships but also to theories of evolutionary mechanisms and adaptive scenarios involved in the origin of major groups, which may be virtually unconstrained when information on the order of acquisition of apomorphies is lacking. For example, given that angiosperms are related to Bennettitales and Gnetales, the fact that the latter groups show evidence of insect pollination (aggregation of sporophylls into flowers, often bisexual) and progenetic acceleration of the reproductive cycle (small seed size, reduced megaspore wall: cf. Crane, 1985) indicates that these features were established well before carpel closure. This in turn requires revision of suggestions that the origin of angiosperms was directly tied to the origin of insect pollination and/or pressures for rapid reproduction (e.g., Stebbins, 1974; Hickey and Doyle, 1977; Doyle, 1978), although it may of course have been related to changes in these factors.

Fossils provide still more evidence on scenarios when other information obtainable from the fossil record is added: data on minimum ages of groups, their geographic distributions, and associated paleoenvironments, including both physical and biotic components (e.g., presence or absence of potential herbivores or pollinators). Thus several lines of evidence support the notion that the origin of coniferopsids was related to aridity. The plesiomorphic seed fern relatives of coniferopsids were centered in wet, tropical, lowland areas, but there are indications that cordaites were dominant in Carboniferous upland environments (Chaloner and Muir, 1968), and the rise of conifers in the Permian of the Euramerican tropical belt was correlated with a shift from wet to semi-arid, monsoonal conditions (cf. Rowley et al., 1985). The inferred shift to a coniferopsid habit

in Gnetales may also be linked to aridity, since Gnetales are centered in presumed arid regions in the Early Cretaceous (Brenner, 1976; Doyle et al., 1982). The somewhat similar distributions of Bennettitales and early angiosperms suggest that aridity may also have been involved in the strong progenetic tendency seen in anthophytes as a whole, and in the independent origin of vessels in angiosperms and Gnetales (Doyle and Donoghue, 1986). In other groups, a shift from manoxylic to "coniferopsid" pycnoxylic stem anatomy seems to be correlated with occupation of temperate areas (glossopterids, corystosperms, *Pentoxylon*, possibly ginkgos). Generally similar conclusions were reached by Meyen (1984), working in a non-cladistic framework. In contrast, modern coniferopsid distributions alone might suggest an origin in the mesic temperate zones, while modern angiosperm distributions have often been cited as evidence for an origin in the wet tropics.

In summary, our analysis indicates that fossil data can be of great value in altering or strengthening cladistically inferred relationships among extant groups, and in providing unique evidence on the sequence of events and ecological factors involved in their origin. Since these effects are strongest in dealing with the isolated major groups that dominate the modern biota, our observations amply justify the high regard in which fossils have been traditionally held by students of macroevolution.

Acknowledgements

We wish to thank Jacques Gauthier, Arnold Kluge, and Tim Roe for discussion of results of their unpublished study on amniote phylogeny, and Wm. Stein for valuable comments on the manuscript.

References

- Arber, E.A.N. and Parkin, J., 1907. On the origin of angiosperms. *J. Linn. Soc. Bot.*, 38: 29-80.
- Arber, E.A.N. and Parkin, J., 1908. Studies on the evolution of the angiosperms. The relationship of the

- angiosperms to the Gnetales. *Ann. Bot.*, 22: 489–515.
- Arnold, C.A., 1948. Classification of gymnosperms from the viewpoint of paleobotany. *Bot. Gaz.*, 110: 2–12.
- Beck, C.B., 1960. The identity of *Archaeopteris* and *Callixylon*. *Brittonia*, 12: 351–368.
- Beck, C.B., 1970. The appearance of gymnospermous structure. *Biol. Rev.*, 45: 379–400.
- Beck, C.B., 1981. *Archaeopteris* and its role in vascular plant evolution. In: K.J. Niklas (Editor), *Paleobotany, Paleoecology, and Evolution*, vol. I. Praeger, New York, N.Y., pp.193–230.
- Beck, C.B., Schmid, R. and Rothwell, G.W., 1982. Stelar morphology and the primary vascular system of seed plants. *Bot. Rev.*, 48: 691–815.
- Bremer, K., 1985. Summary of green plant phylogeny and classification. *Cladistics*, 1: 369–385.
- Brenner, G.J., 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. In: C.B. Beck (Editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York, N.Y., pp.23–47.
- Chaloner, W.G. and Muir, M., 1968. Spores and floras. In: D.G. Murchison and T.S. Westoll (Editors), *Coal and Coal-Bearing Strata*. Oliver and Boyd, Edinburgh, pp.127–146.
- Chamberlain, C.J., 1935. *Gymnosperms: Structure and Evolution*. Univ. Chicago Press, Chicago, 484 pp. (republished by Dover Publications, New York).
- Crane, P.R., 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Mo. Bot. Gard.*, 72: 716–793.
- Cronquist, A., 1968. *The Evolution and Classification of Flowering Plants*. Houghton Mifflin, Boston, Mass., 396 pp.
- Cronquist, A., 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press, New York, N.Y., 1262 pp.
- Donoghue, M.J. and Maddison, W.P., 1986. Polarity assessment in phylogenetic systematics: a response to Meacham. *Taxon*, 35: 534–538.
- Doyle, J.A., 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. *J. Arnold Arbor.*, 50: 1–35.
- Doyle, J.A., 1978. Origin of angiosperms. *Ann. Rev. Ecol. Syst.*, 9: 365–392.
- Doyle, J.A. and Donoghue, M.J., 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot. Rev.* 52: 321–431.
- Doyle, J.A., Jardine, S. and Doerenkamp, A., 1982. *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of Northern Gondwana. *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine*, 6: 39–117.
- Eldredge, N., 1979. Cladism and common sense. In: J. Cracraft and N. Eldredge (Editors), *Phylogenetic Analysis and Paleontology*. Columbia Univ. Press, New York, N.Y., pp.165–198.
- Eldredge, N. and Novacek, M.J., 1985. Systematics and paleobiology. *Paleobiology*, 11: 65–74.
- Engelmann, G.F. and Wiley, E.O., 1977. The place of ancestor–descendant relationships in phylogeny reconstruction. *Syst. Zool.*, 26: 1–11.
- Felsenstein, J., 1978. The number of evolutionary trees. *Syst. Zool.*, 27: 27–33.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39: 783–791.
- Fisher, D.C., 1980. The role of stratigraphic data in phylogenetic inference. *Geol. Soc. Am. Abstr. with Programs*, 12: 426.
- Florin, R., 1938–1945. Die Koniferen des Oberkarbons und des unteren Perms. *Palaeontographica Abt. B*, 85: 1–729.
- Florin, R., 1951. Evolution in cordaites and conifers. *Acta Horti Berg.*, 15: 285–388.
- Fortey, R.A. and Jeffries, R.P.S., 1982. Fossils and phylogeny — a compromise approach. In: K.A. Joysey and A.E. Friday (Editors), *Problems of Phylogenetic Reconstruction*. Syst. Assoc., 21: 197–234.
- Friis, E.M., 1983. Upper Cretaceous (Senonian) floral structures of juglandalean affinity containing *Normapolles* pollen. *Rev. Palaeobot. Palynol.*, 39: 161–188.
- Gardiner, B.G., 1982. Tetrapod classification. *Zool. J. Linn. Soc.*, 74: 207–232.
- Gaussen, H., 1946. *Les Gymnospermes, actuelles et fossiles*. Trav. Lab. For. Toulouse, Tome II Etud. Dendrol., sect. 1, 1(3): 1–26.
- Gingerich, P.D., 1979. The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In: J. Cracraft and N. Eldredge (Editors), *Phylogenetic Analysis and Paleontology*. Columbia Univ. Press, New York, N.Y., pp.41–77.
- Hendy, M.D. and Penny, D., 1982. Branch and bound algorithms to determine minimal evolutionary trees. *Math. Biosci.*, 59: 277–290.
- Hennig, W., 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana, Ill., 263 pp.
- Hennig, W., 1969. *Die Stammesgeschichte der Insekten*. Kramer, Frankfurt, 436 pp.
- Hickey, L.J. and Doyle, J.A., 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.*, 43: 1–104.
- Hill, C.R. and Crane, P.R., 1982. Evolutionary cladistics and the origin of angiosperms. In: K.A. Joysey and A.E. Friday (Editors), *Problems of Phylogenetic Reconstruction*. Syst. Assoc., 21: 269–361.
- Hughes, N.F., 1976. *Palaeobiology of Angiosperm Origins*. Cambridge Univ. Press, Cambridge, 242 pp.
- Jeffries, R.P.S., 1979. The origin of chordaites — a methodological essay. In: M.R. House (Editor), *The Origin of Major Invertebrate Groups*. Academic Press, London, pp.443–477.
- Jeffrey, E.C., 1902. The structure and development of the stem in the Pteridophyta and gymnosperms. *Philos. Trans. R. Soc. London, Ser. B*, 195: 119–146.
- Jeffrey, E.C., 1910. The Pteropsida. *Bot. Gaz.*, 50: 401–414.
- Maddison, W.P., Donoghue, M.J. and Maddison, D.R., 1984. Outgroup analysis and parsimony. *Syst. Zool.*, 33: 83–103.
- Mamay, S.H., 1976. Paleozoic origin of the cycads. *U.S.*

- Geol. Surv. Prof. Pap., 934: 1-48.
- Mapes, G. and Rothwell, G.W., 1984. Permineralized ovulate cones of *Lebachia* from late Palaeozoic limestones of Kansas. *Palaeontology*, 27: 69-94.
- Martens, P., 1971. Les Gnétophytes. *Encyclopedia of Plant Anatomy*, 12(2). Borntraeger, Stuttgart, 295 pp.
- Meacham, C.A., 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. *Taxon*, 33: 26-38.
- Meeuse, A.D.J., 1972. Facts and fiction in floral morphology with special reference to the Polycarpicae. *Acta Bot. Neerl.*, 21: 113-127, 235-252, 351-365.
- Meyen, S.V., 1984. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Bot. Rev.*, 50: 1-112.
- Mickevich, M.F. and Farris, J.S., 1982. Phylogenetic analysis system (PHYSYS) (FORTRAN V software system of cladistic and phenetic algorithms).
- Muller, J., 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Cambridge Philos. Soc.*, 45: 417-450.
- Muller, J., 1981. Fossil pollen records of extant angiosperms. *Bot. Rev.*, 47: 1-142.
- Nelson, G., 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst. Zool.*, 27: 324-345.
- Oliver, F.W. and Scott, D.W., 1903. On *Lagenostoma Lomaxi*, the seed of *Lyginodendron*. *Proc. R. Soc. London B*, 71: 477-481.
- Patterson, C., 1977. The contribution of paleontology to teleostean phylogeny. In: M.K. Hecht, P.C. Goody and B.M. Hecht (Editors), *Major Patterns of Vertebrate Evolution*. Plenum, New York, N.Y., pp.579-643.
- Patterson, C., 1981. Significance of fossils in determining evolutionary relationships. *Ann. Rev. Ecol. Syst.*, 12: 195-223.
- Platnick, N.I., 1977. Cladograms, phylogenetic trees, and hypothesis testing. *Syst. Zool.*, 26: 438-442.
- Rothwell, G.W., 1982. New interpretations of the earliest conifers. *Rev. Palaeobot. Palynol.*, 37: 7-28.
- Rowley, D.B., Raymond, A., Parrish, J.T., Lottes, A.L., Scotese, C.R. and Ziegler, A.M., 1985. Carboniferous paleogeographic, phytogeographic, and paleoclimatic reconstructions. *Int. J. Coal Geol.*, 5: 7-42.
- Schaeffer, B., Hecht, M.K. and Eldredge, N., 1972. Phylogeny and paleontology. *Evol. Biol.*, 6: 31-46.
- Simpson, G.G., 1961. *Principles of Animal Taxonomy*. Columbia Univ. Press, New York, N.Y., 247 pp.
- Stebbins, G.L., 1974. *Flowering Plants: Evolution above the Species Level*. Harvard Univ. Press, Cambridge, Mass., 399 pp.
- Stevens, P.F., 1980. Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.*, 11: 333-358.
- Takhtajan, A.L., 1969. *Flowering Plants: Origin and Dispersal*. Smithsonian Institution, Washington, D.C., 310 pp.
- Upchurch, G.R., 1984. Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland. *Ann. Mo. Bot. Gard.*, 71: 522-550.
- Von Wettstein, R.R., 1907. *Handbuch der systematischen Botanik*, II. Band. Deuticke, Leipzig, Wien, 577 pp.
- Wolfe, J.A., 1973. Fossil forms of Amentiferae. *Brittonia*, 25: 334-355.
- Wolfe, J.A., Doyle, J.A. and Page, V.M., 1975. The bases of angiosperm phylogeny: Paleobotany. *Ann. Mo. Bot. Gard.*, 62: 801-824.
- Young, D.A., 1981. Are the angiosperms primitively vesselless? *Syst. Bot.*, 6: 313-330.