Seed Plant Phylogeny and the Origin of Angiosperms: An Experimental Cladistic Approach

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Abstract

We present a numerical cladistic (parsimony) analysis of seed plants plus progymnosperms, using characters from all parts of the plant body, outgroup comparison, and a method of character coding that avoids biases for or against alternative morphological theories. The robustness of the results was tested by construction of alternative trees and analysis of subsets of the data. These experiments show that although some clades are strongly supported, they can often be related to each other in very different but nearly equally parsimonious ways, apparently because of extensive homoplasy. Our results support Rothwell's idea that conifer-opsids are derived from *Callistophyton*-like platyspermic seed ferns with saccate pollen, but the hypothesis that they evolved from *Archaeopteris*-like progymnosperms and the seed arose twice is nearly as parsimonious. Meyen's division of seed plants into radiospermic and primarily and secondarily platyspermic lines is highly unparsimonious, but his suggestion that ginkgos are related to peltasperms deserves attention. Angiosperms belong among the platyspermic groups, as the sister group of Bennettitales, *Pentoxylon,* and Gnetales, and this "anthophyte" clade is best related to *Caytonia* and glossopterids, although relationships with other combinations of Mesozoic seed fern taxa are nearly as parsimonious. These results imply that the angiosperm carpel can be interpreted as a modified pinnate sporophyll bearing anatropous cupules (=bitegmic ovules), while gnetalian strobili are best interpreted as aggregations of highly reduced bennettitalian flowers, as anticipated by Arber and Parkin and Crane. Our most parsimonious trees imply that the angiosperm line (though not necessarily all its modern features) extended back to the Triassic, but a later derivation of angiosperms from some species of *Caytonia* or Bennettitales, which would be nearly as parsimonious, should also be considered. These results raise the possibility that many features considered key adaptations in the origin and rise of angiosperms (insect-pollinated flowers, rapid reproduction, drought tolerance) were actually inherited from their gymnospermous precursors. The explosive diversification of angiosperms may instead have been a consequence of carpel closure, resulting in increased speciation rates due to potential for stigmatic isolating mechanisms and/or new means of dispersal. DNA sequencing of extant plants and better information on anatomy, chemistry,

sporophyll morphology, and embryology of Bennettitales and Caytoniales and the morphological diversity of Mesozoic anthophytes could provide critical tests of relationships.

Résumé

Nous présentons une analyse cladistique numérique (de parcimonie, ou économie d'hypothèses) des Spermatophytes plus Progymnospermes, utilisant des caractères de tous les organes du corps végétal, la comparaison extra-groupe, et une méthode de codification de caractères qui évite des prédispositions en faveur de ou contre les théories morphologiques alternatives. La solidité des résultats a été testé par la construction d'arbres phylétiques alternatifs et l'analyse de sous-ensembles des données. Selon ces expériences, certains phylums sont bien appuyés, mais ils peuvent être reliés de façons très différentes mais presque également économiques, apparemment à cause d'homoplasie répandue. Nos résultats confirment le concept de Rothwell, selon lequel les Coniféropsides sont dérivées de Ptéridospermes platyspermiques à pollen saccate proches de *Callistophyton,* mais l'hypothèse d'une dérivation de Progymnospermes proches d'*Archaeopteris* et d'une origine diphylétique de la graine est presque aussi économique. La division de Meyen des Spermatophytes en lignées radiospermiques et primairement et secondairement platyspermiques est très peu économique, mais son concept d'une affinité entre les Ginkgoales et les Peltaspermes mérite de l'attention. Les Angiospermes se situent parmi les groupes platyspermiques, comme groupe-frère des Bennetti-tales, *Pentoxylon,* et Gnetales, et le phylum ainsi constitué ("Antho-phytes") est le mieux lié à *Caytonia* et aux Glossoptérides, bien que des rapports avec d'autres combinaisons de taxons de Ptéridospermes mésozoïques soient presque aussi économiques. Ces résultats indiquent que le carpelle des Angiospermes peut être interprété comme une sporophylle pennée modifiée portant des cupules anatropes (=ovules bitégumentés), puisque les strobiles des Gnetales sont le mieux interprétés comme des agglomérations de fleurs bennettitaliennes fort réduites, comme l'a proposé Arber et Parkin et Crane. Nos arbres phylétiques les plus écono-miques supposent que la lignée des Angiospermes (mais pas forcément tous ses traits modernes) s'étend jusqu'au Trias, mais une origine plus récente à partir de quelque espèce de *Caytonia* ou de Bennettitales, hy-pothèses presque aussi économiques, doit aussi être considérée. Ces ré-sultats suggèrent que plusieurs traits considérés comme des adaptations-clés dans l'origine ou l'expansion des Angiospermes (fleurs entomophiles, rapidité de reproduction, tolérance de sécheresse) étaient en fait hérités de leurs ancêtres gymnospermiques. La diversification explosive des An-giospermes pourrait plutôt être une conséquence de la clôture du carpelle,

conduisant à un taux de spéciation élevé dû au potentiel pour des mécanismes d'isolement stigmatiques et/ou de nouveaux moyens de dispersion. L'étude de séquences d'ADN des végétaux actuels et de meilleurs renseignements sur l'anatomie, la phytochimie, la morphologie des sporophylles, et l'embryologie des Bennettitales et Caytoniales pourraient fournir des testes critiques de rapports phylétiques.

I. Introduction

In recent years there has been renewed interest in the old problem of the origin and early evolution of angiosperms, largely as a result of paleobotanical studies on Cretaceous sediments. Although there is more agreement now than 25 years ago concerning the timing and pattern of the early diversification of angiosperms, the question of their origin remains controversial. At the same time, there has been increased interest in the relationships among other major seed plant groups (gymnosperms), stimulated by recognition of the Devonian progymnosperms and new information on Carboniferous seed ferns. Although these problems have often been considered separately, we suggest that they are best considered together: an understanding of phylogenetic relationships among seed plants is critical in assessing both basic conditions within angiosperms and evolutionary events and processes in their origin. Hence in this paper we will evaluate hypotheses on seed plant phylogeny using numerical cladistic methods and consider implications for the angiosperm problem.

A. RELATIONSHIPS AMONG MAJOR SEED PLANT GROUPS

Beginning early in this century, the idea developed that gymnosperms can be divided into two major groups, cycadopsids and coniferopsids (Arnold, 1948; Chamberlain, 1935; Sporne, 1965). Cycadopsids include the living cycads and several extinct groups, the most primitive being the so-called seed ferns or pteridosperms. They typically have relatively unbranched, manoxylic stems; basically pinnately compound leaves (pteridophylls); and radially symmetrical (radiospermic) seeds borne on leaf homologs. Coniferopsids include conifers, the Paleozoic cordaites (shown to be related to conifers by Florin, 1951), and ginkgos. They typically have highly branched, pycnoxylic stems; simple leaves, either one-veined (microphylls) or with several equal dichotomizing veins and no midrib (sphenophylls); and bilaterally symmetrical (platyspermic) seeds borne on modified axillary branches.

Ideas on the relationship between cycadopsids and coniferopsids remained vague until recognition of the Devonian "progymnosperms," which had gymnospermous anatomical advances (secondary xylem and phloem, periderm) but which still reproduced by spores (Beck, 1960). Elucidation

of the morphology of progymnosperms led gradually to the concept that both gymnosperm lines could be derived from them, but by different processes, and from different subgroups (Beck, 1966, 1970, 1971, 1981; Meeuse, 1963). According to this hypothesis, cycadopsids transformed the leafy (sphenophyll-bearing) branch systems of progymnosperms into compound fronds, by planation and a shift to appendicular status, while coniferopsids left them essentially unchanged, except for reduction of sphenophylls to microphylls in some groups and a shift from apical to axillary branching. Since some early seed ferns were protostelic, cycadopsids were presumably derived from some protostelic member of the progymnosperms (Aneurophytales), rather than the more advanced Late Devonian genus *Archaeopteris,* which already had a eustele. In contrast, coniferopsids show evidence of a closer relationship with *Archaeopteris*: they are all eustelic, and the vegetative branch systems of early conifers and the fertile branch systems of both cordaites and conifers are constructed on an *Archaeopteris*-like plan. Such relationships would imply that the seed originated twice, which would be consistent with the different symmetry of the seed in the two groups.

The idea that cycadopsids and coniferopsids represent two natural groups independently derived from progymnosperms, which we will hereinafter refer to as the "Beck hypothesis," has recently been challenged by Rothwell (1981, 1982). Based on the many conifer-like features of the recently recognized Late Carboniferous seed fern *Callistophyton* (e.g., platyspermic ovules, saccate pollen, frequent axillary branching), Rothwell proposed that conifers (and possibly cordaites) were derived from platyspermic seed ferns. Although he formulated this concept primarily in terms of conifers, we will hereinafter use the expression "Rothwell hypothesis" to apply to coniferopsids as a whole, which would imply that the seed originated only once. He argued that this scenario is more consistent with the stratigraphic record, since there is a considerable time gap between *Archaeopteris* (Late Devonian) and the first cordaites and conifers (Late Carboniferous), during which all known seed plants are of the seed fern type. This view poses major morphological problems, since *Callistophyton* had large, fern-like fronds rather than microphylls or sphenophylls. Noting that *Callistophyton* also had pointed cataphylls, Rothwell suggested that origin of a conifer-like morphology might have occurred by heterochrony: suppressing development of the fronds and continuing to produce cataphylls throughout the life of the plant. Major changes in branching habit and stem anatomy might then be expected for functional and/or developmental reasons.

The Beck hypothesis has also been challenged by Meyen (1984). Like Rothwell, he proposed that the groups conventionally included in coniferopsids were derived from seed ferns, but he recognized two platyspermic

lines: the primitively platyspermic Ginkgoopsida, including Carboniferous Calamopityaceae, *Callistophyton,* Permian peltasperms and glossopterids, ginkgophytes, Mesozoic seed ferns, and possibly *Pentoxylon* and *Ephedra*; and the secondarily platyspermic Pinopsida, including cordaites and conifers. He derived the Pinopsida from primitive members of the radiospermic Cycadopsida (Lagenostomales, or lyginopterid seed ferns), in which he also included medullosans, cycads, Bennettitales, and tentatively *Welwitschia, Gnetum,* and angiosperms, accepting the proposed homology of the free integument of medullosans with the cupule of lyginopterids (Walton, 1953) and extending this to cordaites and other groups. His analysis has been criticized by Beck (1985), Miller (1985), and Rothwell (1985), for insufficient evidence for reconstruction of certain key forms, over-emphasis on seed characters, and various other reasons.

B. RELATIONSHIPS OF ANGIOSPERMS TO OTHER SEED PLANTS

Ideas on the relationships of angiosperms to gymnosperms have varied as much as ideas on relationships among gymnosperm groups. The first two comprehensive theories on this subject were developed early in this century, before clear formulation of the distinction between cycadopsids and coniferopsids.

One view, widely (though inaccurately: Meeuse, 1972b) associated with the Englerian school of systematics, is that the angiosperms were derived from the advanced gymnosperm order Gnetales, represented today by *Ephedra, Welwitschia,* and *Gnetum* (Wettstein, 1907). The Gnetales are unique among gymnosperms in having so many features otherwise restricted to angiosperms. All three genera have vessels in the wood and reproductive structures (compound strobili) made up of minute flower-like units, with either a perianth and a whorl of more or less fused microsporophylls or a terminal ovule surrounded by an additional envelope. *Gnetum* is remarkably dicot-like in habit and leaf architecture, and *Welwitschia* and *Gnetum* show almost as much reduction of the male gametophyte as in angiosperms, a partially free-nuclear female gametophyte, and cellular embryogeny (cf. Martens, 1971). Wettstein homologized the compound strobili of Gnetales with the inflorescences (catkins) of the wind-pollinated Amentiferae, Pandanaceae, and Piperales, which are also made up of apetalous, unisexual flowers. He interpreted the showy, insect-pollinated, bisexual flowers of *Magnolia* and other groups as pseudanthia, derived by aggregation of unisexual units. This would imply that the first angiosperms were wind-pollinated, and that insect pollination arose later during the radiation of the group.

A competing view was proposed by Arber and Parkin (1907, 1908), stimulated by recognition that the Mesozoic cycadopsid group Bennet

titales had strikingly flower-like reproductive structures, sometimes bisexual, with a perianth, a whorl of pinnate microsporophylls, and a central ovuliferous receptacle. They homologized these structures with the flowers of *Magnolia* and argued that the flowers of Amentiferae were secondarily reduced and aggregated as a result of a return to wind pollination. Seeds of Bennettitales were borne singly on simple stalks, interspersed with interseminal scales, rather than on any structure comparable to an angiosperm carpel, and the microsporophylls were whorled and usually fused basally. Therefore, rather than deriving angiosperms directly from Bennettitales, Arber and Parkin proposed that the two groups evolved from a hypothetical common ancestor with a "pro-anthostrobilus" bearing pinnate micro- and megasporophylls. In Bennettitales, the megasporophylls were presumably reduced; in angiosperms, the microsporophylls. Like Wettstein, Arber and Parkin assumed that Gnetales were related to angiosperms (as their immediate sister group), but they interpreted the "flowers" of Gnetales as reduced from bisexual strobili (as in Amentiferae), citing among other evidence the presence of an abortive terminal ovule in the staminate flowers of *Welwitschia.*

Both these theories have subsequently fallen into wide disfavor. Relationships between angiosperms and Gnetales, assumed under both theories, have come under especial criticism. First, closer examination suggests that many of the common features of the two groups originated independently. For example, some modern angiosperms, such as the magnoliid family Winteraceae, lack vessels in the wood; if this condition is primitive (as is generally assumed), it implies that angiosperms were derived from some group without vessels, not with them. Furthermore, vessel members in the two groups appear to be derived from different kinds of tracheids: Gnetales have vessel members with perforations that intergrade with circular bordered pits, while primitive angiosperms have tracheids with scalariform pitting or vessel members with scalariform perforations (Bailey, 1944; Thompson, 1918). Doubts concerning a direct connection between Gnetales and Amentiferae have also come from increasing recognition of putatively ancestral characters in magnoliid dicots (vesselless wood, gymnosperm-like monosulcate pollen, leaf-like carpels and stamens) and derived characters in Amentiferae (advanced vessels, triporate pollen). In the past 25 years, these ideas on evolution within the angiosperms have been strengthened by paleobotanical studies of Cretaceous rocks. The first recognizable angiosperm pollen is monosulcate, while amentiferous-type pollen does not appear until later, apparently as the culmination of a long series of modifications, and the leaf record reveals consistent trends (Doyle, 1969, 1978; Doyle & Hickey, 1976; Muller, 1970, 1981; Upchurch, 1984).

In addition, several lines of evidence have led to the idea that Gnetales

are related to coniferopsids, while angiosperms are related to cycadopsids. For example, Gnetales have circular bordered pits in the metaxylem and even the protoxylem, like conifers and *Ginkgo*, whereas metaxylem tracheids in angiosperms have scalariform pitting, as in cycadopsids (Bailey, 1944). Eames (1952) homologized the flowers of *Ephedra* with the axillary fertile short shoots of *Cordaites*, equating the perianth of the staminate flower and the envelope around the seed in *Ephedra* with the sterile scales on the short shoots of *Cordaites*. He rejected relationships of *Ephedra* with *Welwitschia* and *Gnetum*, based largely on ontogenetic and anatomical arguments that the ovule is appendicular in *Ephedra* but truly terminal in *Gnetum* and *Welwitschia* and on the bennettitalian-type (syndetocheilic) stomata of the latter two genera (Florin, 1931). However, his ontogenetic arguments are not confirmed by more recent studies (Martens, 1971), and other authors have noted that *Welwitschia* and *Gnetum* have the same coniferopsid wood features as *Ephedra* and that their reproductive structures too can be interpreted as modifications of a coniferopsid plan (Bailey, 1944; Bierhorst, 1971; Doyle, 1978). Conversely, the leaf-like carpels of magnoliids suggest relationships with cycadopsids, in which seeds are usually borne on obvious leaf homologs, and within seed plants scalariform secondary xylem pitting is largely restricted to angiosperms, Bennettitales, and some cycads.

Although evidence for primitive features in magnoliids favors many of Arber and Parkin's (1907) ideas concerning angiosperm evolution, and Bennettitales and vesselless angiosperms are almost identical in wood anatomy, their concept of a relationship between angiosperms and Bennettitales has been widely dismissed. Reasons for this rejection are somewhat unclear, although much skepticism has centered on the fact that Arber and Parkin relied so heavily on a purely hypothetical prototype that has remained undiscovered. Many authors have emphasized the morphological differences between the parts making up the flowers in the two groups and regarded their similarities as convergent adaptations to similar selective pressures, presumably insect pollination.

It should be noted that these arguments are not universally accepted. For example, Meeuse (1963, 1972a, 1972b) has proposed a highly modified version of Wettstein's theory, which interprets angiosperm reproductive structures as derived from a polyaxial "anthocorm" system and considers Gnetales and Piperales links between "higher cycadopsids" and angiosperms. Young (1981) challenged the traditional view that the first angiosperms were vesselless, arguing on the basis of a cladistic analysis of primitive angiosperms that it is more parsimonious to assume that vessels were lost in several early lines. Muhammad and Sattler (1982) found similar scalariform perforations in vessel elements of *Gnetum* and angiosperms and suggested that (some) angiosperms might be derived

from Gnetales after all. Similarly, Takhtajan (1969) and Ehrendorfer (1976) continue to argue that angiosperms share a common ancestry with Bennettitales, and that Gnetales are highly modified bennettitalian derivatives. However, most recent discussions of the origin of angiosperms have focused instead on seed ferns, in which sporophylls are less reduced (Cronquist, 1968; Doyle, 1978; Stebbins, 1974).

Two Mesozoic seed fern families that have attracted particular attention are Caytoniaceae, a widespread Triassic to Cretaceous group with palmately compound leaves, simple reticulate venation, and once-pinnate megasporophylls bearing reflexed cupules along the rachis; and Corystospermaceae, a Gondwana Triassic group with more fern-like leaves and bipinnate megasporophylls. Early attempts to homologize the cupules of these forms with carpels (Thomas, 1925) were unsuccessful (the cupules appear to be modified leaflets rather than whole sporophylls borne on a stem), but several authors have pointed out that reduction to one ovule per cupule (already seen in corystosperms) would result in a structure like the anatropous, bitegmic ovule of angiosperms, with the outer integument corresponding to the cupule wall (Doyle, 1978; Gaussen, 1946; Stebbins, 1974). The carpel itself could then be derived from the sporophyll rachis by expansion and folding to enclose the ovules. Following ideas of Gould (1977), Doyle (1978) argued that the changes in relative proportions and reduced size of angiosperm structures implied by this scenario suggest an origin through progenesis (paedomorphosis resulting from precocious maturation). Since Gould associates progenesis with selection for high reproductive rates (*r*-selection), this hypothesis is consistent with the idea that early angiosperms were weedy colonizing species, as proposed by Stebbins (1974) and supported by Doyle and Hickey (1976) on Cretaceous fossil evidence (restriction to stream-margin facies, leaf morphology, etc.).

Another much-discussed group is the predominantly Permian Glossopteridales of Gondwana, considered coniferopsids by Schopf (1976) but seed ferns by Gould and Delevoryas (1977) and most subsequent authors. Glossopterids had simple leaves with simple reticulate venation and ovulate structures consisting of a leaf with one or several cupule-like structures on its adaxial side. Stebbins (1974) and Retallack and Dilcher (1981) have argued that the ovulate structures could be transformed into an angiosperm carpel by reduction of the ovules per cupule to one (seen in *Denkania*) and folding of the leaf. A disadvantage of this hypothesis is that it involves a major stratigraphic gap between glossopterids and the first known angiosperms (Doyle, 1978).

This brief review in no way exhausts existing hypotheses on seed plant relationships and the origin of angiosperms. For example, many authors support a polyphyletic origin of angiosperms (Hughes, 1976; Krassilov, 1977; Meeuse, 1963, 1972a, 1972b). Hughes (1976) and Krassilov (1977)

have proposed that some angiosperms were derived from the Mesozoic ginkgophyte group Czekanowskiales, which had seeds enclosed in bivalved capsules. Burger (1981a) has even challenged the general assumption that angiosperms are derived from some group of gymnosperms, arguing that monocots are more primitive than dicots in many respects and suggesting homologies between monocots and lower vascular plants.

C. PREVIOUS CLADISTIC STUDIES

Recently, the question of seed plant relationships has been put into new perspective by use of cladistic methods. Cladistic analysis attempts to reconstruct the branching pattern of phylogeny, and hence to recognize clades or monophyletic groups (in the strict sense of Hennig, 1966), from the distribution of shared derived characters (synapomorphies). The most widely accepted method for determining ancestral vs. derived character states (polarity) is outgroup comparison: if one of two character states is restricted to the group in question but the other occurs in related groups, the latter is assumed ancestral. Of course, convergences and reversals (homoplasy) often lead to character conflicts and competing hypotheses of relationship; such conflicts are usually resolved using the criterion of parsimony, with preference given to the scheme that requires the fewest character state changes. It should be noted that parsimony analysis does not assume that evolution necessarily follows the most parsimonious path; it is simply a method of finding the hypothesis of relationships that is best supported by the totality of known characters, given certain very general assumptions on character behavior (for varying views on the validity of this assertion, see Farris, 1983; Felsenstein, 1983; Sober, 1983, 1985). By considering the number of steps in all characters, parsimony analysis is capable of recognizing groups in which some members lack "defining" features of the group as a whole because of secondary loss or modification; in this respect it resembles the "congregational analysis" of Meyen (1984), but it is less subjective.

Of the attempts to apply cladistic methods to seed plant phylogeny, the first two, by Parenti (1980) and Bremer and Wanntorp (1981), need not be discussed in detail. Parenti relied on superficial resemblances, and her study has been adequately criticized by Smoot et al. (1981) and Young and Richardson (1982). Bremer and Wanntorp left the interrelationships of extant cycads, ginkgos, conifers, Gnetales, and angiosperms unresolved, classifying them all at the same rank.

A far more ambitious analysis was performed by Hill and Crane (1982). Still treating extant groups only, they favored a scheme in which angiosperms are the sister group of conifers plus Gnetales, while cycads plus *Ginkgo* are the sister group of the angiosperm-conifer-gnetalian clade.

This scheme contrasts with the common interpretation of coniferopsids (including ginkgos) and cycadopsids as sister groups, Gnetales as coniferopsid derivatives, and angiosperms as cycadopsid derivatives. However, these results are questionable for several reasons. One set of problems concerns character analysis (see also **Appendix II and III**), several of which are illustrated by the four characters that support the angiosperm-conifer-gnetalian clade. In one character, pycnoxylic anatomy, polarity is doubtful, as a result of not considering fossil groups: outgroup comparison with progymnosperms would suggest that pycnoxylic is ancestral in seed plants, not derived. Two other characters, siphonogamy and non-motile sperm, appear to be aspects of the same character (i.e., they are redundant); treating them separately gives excessive weight to what may be a single change. The fourth character, presence of strobili, is too vaguely defined, since it refers to structures made up of very different-looking parts in different groups. Other problems concern scoring of groups; thus angiosperms are scored as pycnoxylic, but presumably primitive dicots have multiseriate rays and xylem parenchyma, characters usually associated with manoxylic construction. Furthermore, although Hill and Crane's scheme appears to be supported by a large amount of information (50 characters), over half the characters used are either synapomorphies of all seed plants or derived characters restricted to angiosperms or other terminal groups (autapomorphies) or to Gnetales, and are therefore not informative in determining relationships among major groups. Hill and Crane also omitted a large number of potentially relevant characters. For example, except for presence of several vein orders in *Gnetum* and angiosperms and striate pollen in *Ephedra* and *Welwitschia*, features of leaf architecture and anatomy, organization of the ovule-bearing structures, and pollen morphology are poorly represented. Ideally, given the basic features of the whole group, it should be possible to derive a synoptic picture of the morphology of any terminal group by tracing the changes from the base of a cladogram to the top. Finally, Hill and Crane (1982) did not take advantage of computer-assisted (numerical cladistic) methods, which are all but essential when dealing with complex groups where character conflicts are common. Without numerical methods, it is easy to concentrate on a few favored characters and to overlook more parsimonious alternative relationships.

This analysis was subsequently completely redone by Crane (1985a, 1985b), taking into account fossil as well as living groups. He concluded that coniferopsids were derived from platyspermic seed ferns (cf. Rothwell, 1982), and he separated Gnetales from the coniferopsids and placed them together with angiosperms, Bennettitales, and *Pentoxylon* in a clade related to Mesozoic seed ferns. He laid much emphasis on possible homologies of the cupules of Mesozoic seed ferns, the outer integument of

the angiosperm ovule, and the layer that surrounds the ovule in *Pentoxylon* and some Bennettitales. As Crane noted, his results reconcile Arber and Parkin's (1907, 1908) views on relationships of angiosperms, Bennettitales, and Gnetales and more recent comparisons between angiosperms and Mesozoic seed ferns.

Many of the problems in character analysis seen in Hill and Crane (1982) were corrected in Crane's (1985a) study, but others remain. Crane still omitted many potentially useful characters (e.g., only seven characters out of 38 are vegetative, and three of these are autapomorphies), including several cited as evidence for alternative relationships (e.g., similarities in branching pattern in *Archaeopteris* and coniferopsids, anatomical similarities between Gnetales and coniferopsids) and several characters of Hill and Crane (1982), such as thick nucellar cuticle and the Mäule reaction. Thus many connections in his trees are supported by very few characters. In other cases, his interpretation of characters predisposes the analysis toward particular theories; for example, he treated platyspermic seeds as derived from radiospermic, which biases in favor of a single origin of the seed. Bennettitales were grouped with *Pentoxylon* based on heads composed of erect, uniovulate "cupules," but these are features that may well have existed in ancestors of Gnetales but were later lost or obscured as a result of general floral reduction. These aspects of his analysis make it difficult to judge how much more strongly supported his scheme is than are alternative ones (i.e., how robust it is). Finally, although Crane used a computer to generate his final cladograms, his methods of scoring groups are sometimes questionable. In particular, when information on a character in fossil groups was lacking, he often assumed that the ancestral state was present. This policy was intended to avoid bias, but it can lead to unwarranted conclusions. For example, angiosperms are linked with Gnetales on a single character, siphonogamy, but as Crane acknowledges, there is no reason to assume that this feature did not exist in the next most closely related groups, Bennettitales and *Pentoxylon*. As discussed below, a more appropriate procedure in such cases is to score the fossils as unknown (X).

Although we find previous cladistic studies of seed plants unsatisfying in many respects, we do not mean to criticize the use of cladistic methods, or to imply that these studies are especially weak. We agree that the only way to resolve the question of the origin of angiosperms is in the context of a general understanding of seed plant relationships, and that the best approach to this goal is through cladistic analysis, since this is the most explicit and logically sound method of phylogeny reconstruction. In fact, previous cladistic studies can be criticized in such detail because they have the great virtue of being explicit, and because they specify a criterion

(parsimony) by which alternative hypotheses can be compared and some preferred over others.

In an attempt to overcome these problems, we undertook the present numerical cladistic study, which differs from previous analyses in several respects. First, we attempted to amass as many potentially informative (non-autapomorphic) characters as possible from all parts of the plant body, and to code them in ways consistent with the strongest versions of major competing theories of morphological evolution. In addition, in order to assess the robustness of our results and the relative merits of alternative hypotheses, we adopted an experimental approach, asking the computer not only to produce the most parsimonious tree(s), but also to determine the length of alternative trees, and to generate trees from different subsets of the data. Results of one of our earlier analyses are presented elsewhere, in a discussion emphasizing the problem of relationships between angiosperms and Gnetales (Doyle & Donoghue, 1986). As discussed in the next section and **Appendix II**, differences between results reported in that paper and here are due largely to recoding of sporophyll characters in cycads and ovule and cupule characters in Bennettitales, *Pentoxylon*, and angiosperms, based on information and arguments presented by Crane (1985a) and recognition of subtle biases in our previous character codings. Elsewhere we have summarized results of this study that relate to the origin of angiosperms (Doyle & Donoghue, in press a), and we have used the data matrix as the basis of an experimental assessment of the general importance of fossil groups in phylogeny reconstruction (Doyle & Donoghue, in press b).

II. Methods

A. CHOICE OF TAXA

In the present study, we used the 20 terminal taxa listed in Table I and defined, with discussion of problems and possible autapomorphies, in **Appendix I**. Choice of taxa was necessarily a compromise based on several factors: a desire to represent all major seed plant groups and to recognize only monophyletic groups, the varying quantity and quality of information available on different groups (especially fossils), and potential relevance of groups to major problems of seed plant relationships, particularly the origin of angiosperms. Thus we treated *Ephedra*, *Welwitschia*, and *Gnetum* as separate taxa because we hoped to test the recurrent suggestion that the Gnetales are polyphyletic. We split up another conventional taxon, the seed ferns, because they are presumably paraphyletic—a grade taxon, some members of which are more closely related to various "higher" groups than to each other. Similarly, rather than considering only seed

Table I

Terminal taxa used in this study, with abbreviations used in figures and Table II

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

plants, we included two groups of progymnosperms (*Aneurophyton*, *Archaeopteris*), because of the possibility that cycadopsids and coniferopsids are derived independently from progymnosperms. Remarkably, the resulting group (progymnosperms plus seed plants) seems to have no name; Crane (1985b) recognized it but as an "unnamed taxon." We propose the informal term lignophytes (from the presence of secondary xylem in all but some derived members).

Within both progymnosperms and seed ferns, many conventionally recognized subgroups may themselves be paraphyletic. For example, Aneurophytales probably include ancestors of Archaeopteridales and seed plants, and Meyen (1984) argued that the Peltaspermaceae, as he defined them, include ancestors of ginkgophytes and Mesozoic seed ferns. However, because information on various organs of many members of these groups is lacking, it would be premature to attempt to sort them into assuredly monophyletic taxa. In such cases, we preferred to sacrifice our goal of representing all groups, and instead selected one particularly well-reconstructed or phylogenetically critical member for analysis (e.g., *Aneu-*

rophyton, *Peltaspermum*), excluding less completely known forms. This procedure should not lead to misconceptions as long as it is realized that conclusions on relationships apply only to the member chosen, and that other members may have somewhat different cladistic relationships. Excluded groups can be added to future analyses as information accumulates. It is possible that some of the resulting groups are still paraphyletic, since not all of them have definite autapomorphies (see **Appendix I**), but this should not cause problems as long as they are homogeneous for the characters being considered, since then there are no characters that could unite some of their members with any other taxon.

The application of these criteria may be illustrated by the medullosan seed ferns, which include both protostelic forms, such as *Quaestora* and *Sutcliffia* (Mapes & Rothwell, 1980), and *Medullosa*, which has an unusual type of eustele with internal as well as external secondary xylem. The latter stelar type is also seen in other groups (corystosperms, *Pentoxylon*). To allow for the possibility that this similarity is evidence for a direct relationship with *Medullosa* (which would make medullosans in the traditional sense paraphyletic), we did not want to treat medullosans as a single group, which would then have to be coded as protostelic. One solution would be to include both *Medullosa* and the protostelic types in the analysis as separate taxa. We did so in several preliminary analyses, but we finally excluded the protostelic forms because information on so many of their organs is lacking (which made their position unstable) and because omitting them did not significantly affect the results. However, because of the possible close relationship of *Quaestora* and *Sutcliffia* to *Medullosa*, we coded the *Medullosa*-type stele as derivable by one step from either a protostele or a normal eustele (see **Appendix II**).

In one case, we did include a group that is almost surely paraphyletic, the "multiovulate lyginopterids" of the Early Carboniferous. No one member has been reconstructed with confidence, yet the group as a whole is of great significance in that it includes the earliest known seed plants. In our previous paper (Doyle & Donoghue, 1986), we used Long's (1979) reconstruction of *Pitus* (with protostelic stems and multiovulate cupules and microsynangia borne on three-dimensional branch systems at the continuation of the rachis of a bifurcate frond) as a representative of this group. Long's reconstruction has been questioned by A. C. Scott and G. W. Rothwell (pers. comm.) as based on insufficient evidence for association of organs. However, all the distinctive features of the reconstruction are known for other Early Carboniferous seed ferns (cf. Beck, 1970; Sporne, 1965; Stewart, 1983), and since they appear to be primitive on outgroup comparison with progymnosperms, they were presumably originally associated (unless seed ferns are polyphyletic). This presumption is sup-

ported in part by the recent report by Rothwell and Erwin (1986) of association of Late Devonian seed-bearing cupules with protostelic stems and fern-like leaves.

In cases where the amount of information on various organs is marginal, our decision on whether or not to include groups was based on their potential relevance to angiosperm relationships. For example, of four groups in which roughly equal numbers of characters are unknown, we included *Caytonia* and glossopterids, because of their crucial role in discussions of angiosperm origins, but excluded two very interesting Permian coniferopsid groups, *Buriadia* (Pant & Nautiyal, 1967) and Angaran "cordaites" (Meyen, 1984), which are unlikely to be related to angiosperms. However, we did not include the Mesozoic ginkgophyte order Czekanowskiales, even though Krassilov (1977) has proposed that they were ancestral to angiosperms, because still more key aspects of their morphology are unknown or obscure; furthermore, reappraisal of those characters that are available suggests that they are less distinct from Ginkgoales than has been thought (cf. Meyen, 1984).

While subdivision of paraphyletic groups resulted in many small taxa, we left several large, diverse groups such as conifers and angiosperms undivided because they have so many apomorphies that they can be safely assumed to be monophyletic. In order to score such groups, it is necessary to determine basic conditions within them. In most cases these are clear from comparison with any plausible outgroups (e.g., monosulcate pollen in angiosperms), or from hypothesized relationships within the group. Often, polarities within groups are corroborated by the stratigraphic record. Thus we used magnoliid dicots and pre-Albian fossils as guides in coding angiosperms, and Permo-Carboniferous Lebachiaceae in coding conifers. In future studies, it could be instructive to repeat the analysis with alternative assumptions concerning basic conditions.

Since many authors have questioned whether angiosperms are monophyletic (e.g., Hughes, 1976; Krassilov, 1977; Meeuse, 1963, 1972a, 1972b), it is worth noting that we were able to find at least nine apomorphies that unite them: sieve tubes and companion cells derived from the same initials, stamens with two lateral pairs of pollen sacs, a closed carpel with stigmatic pollen germination, a hypodermal endothecium in the anther, lack of a laminated endexine, a megaspore wall without sporopollenin, a three-nuclear male gametophyte with neither prothallials nor a sterile cell, a megagametophyte with only eight nuclei (or various related conditions), and double fertilization with associated endosperm formation. A few angiosperms lack some of these conditions, but the exceptions seem well enough nested within angiosperm groups to assume that they represent secondary reversals or elaborations (e.g., the open carpels of *Reseda* in the Capparales). Some of these characters could conceivably exist in fossil

gymnosperm groups, but as yet there is no direct evidence of this. In order to support a polyphyletic origin of angiosperms, it must be shown that these characters are outweighed by synapomorphies between particular angiosperm subgroups and different gymnosperm groups. Again, the assumption that angiosperms are monophyletic can and should be tested in future cladistic analyses of gymnosperms plus angiosperms split into potentially independent subgroups.

B. CHARACTER ANALYSIS AND CODING

Choice of characters in cladistic analysis involves at least preliminary decisions on homology. We use the term homology to designate traits inherited from a common ancestor (including all their evolutionary transformations). Potential homology may be recognized on the basis of similarity, by consideration of positional and developmental relationships of the structures in question (Kaplan, 1984). However, structures with similar positional and developmental relations can arise independently; conversely, it seems likely on theoretical grounds that changes in the timing of activation of the genetic program responsible for the production of a structure may lead to violation of former positional relationships (heterotopy, a process stressed by Meyen, 1984). Since, in the final analysis, assessment of homology is assessment of common ancestry, the ultimate test of homology is congruence with the totality of evidence on phylogenetic relationships. In practice, morphological analysis of characters and cladistic analysis tend to illuminate each other reciprocally—results of preliminary phylogenetic analysis may lead to closer examination of characters, which may reveal previously unrecognized similarities or differences that can be taken into account in the next round of analysis.

In the case of seed plants, several alternative homologies have been proposed for many structures, with varying degrees of plausibility, and it would be easy to reject possibilities prematurely because of unconscious preference for one or another morphological theory or some overly strict criterion of similarity. Toward our goal of testing alternative hypotheses of seed plant evolution in as unbiased a way as possible, we have allowed relatively wide leeway in treating similarities as potential homologies to be included in the matrix. In only a few cases did we reject characters after preliminary cladistic analysis, when we realized that there were strong positional or developmental reasons why they should not have been included in the first place (e.g., the outer integument of Gnetales and angiosperms: see **Appendix III**). In certain cases where the morphology of structures is particularly obscure or controversial (e.g., ovule symmetry in angiosperms, "sporophylls" of glossopterids), or where there is controversy over which of two states is primitive within a group (e.g., presence

or absence of vessels in angiosperms), we have attempted to avoid bias by treating the character state as unknown (see below).

In numerical methods of the sort used in this study, characters are coded in binary form: 0 (which we used uniformly for the ancestral state), 1 (the derived state), and X (missing data, which takes on the value that gives the most parsimonious result for a given position of a taxon). Multistate characters are represented by additive binary coding (cf. Brooks, 1984); thus a multistate character with a linear series of three states is binary-coded as 00, 10, 11; independent origin of two derived states is coded as 00, 10, 01. In our final analysis, we scored terminal taxa for 62 binary characters (Table II), of which 20 represent eight multistate characters; 24 of our binary characters are vegetative, 38 reproductive. They include characters used by Hill and Crane (1982) and Crane (1985a) that we consider meaningful and many new ones. Characters are defined and discussed in detail in **Appendix II**, along with justification of scoring of taxa.

In **Appendix III**, we list characters that we considered using but did not, including all such characters used by Hill and Crane (1982) and Crane (1985a), and discuss reasons for rejecting them. We consistently excluded autapomorphies: although such characters are important in determining that the terminal taxa used are monophyletic (and are thus listed in **Appendix I**), they contribute nothing to understanding cladistic relationships among groups (although they do indicate that other groups cannot be "derived from," i.e., nested within, them without addition of steps), and they give a false sense of the amount of information and character congruence present in the matrix. We also attempted to eliminate redundant characters, i.e., characters that are correlated for developmental-genetic reasons; coding such characters separately is equivalent to weighting what is actually a single change at a more fundamental level. We usually inferred that characters were redundant when they (1) changed simultaneously on cladograms obtained in preliminary analyses and (2) could be plausibly attributed to the same morphogenetic factors (e.g., substitution of circular bordered for scalariform pitting in the metaxylem and extension of isolated circular bordered pits into the protoxylem in conifers, ginkgos, and Gnetales; opposite phyllotaxy and opposite arrangement of reproductive structures in Gnetales). A problem arises with characters such as architecture of the male and female reproductive structures (25–30), which change in concert in most Paleozoic groups but become uncoupled in Mesozoic groups such as Bennettitales: some developmental correlation is surely present, but it is clearly not absolute, and lumping the characters would result in loss of potentially useful information. Our policy was to treat such characters as separate, but to note evidence for partial correlation when evaluating cladograms of similar parsimony. We eliminated

other characters because they are so irregularly distributed that basic conditions within groups are uncertain, or because information on them is missing in critical taxa (e.g., cortical fiber strands, abaxial vs. adaxial ovule position). Some such characters may turn out to be useful in the future, with better information on distribution and polarity.

We determined polarities by outgroup analysis (Maddison et al., 1984), which necessitated a preliminary analysis of relationships among vascular plants as a whole (Fig. 1). This analysis is generally consistent with the views of Banks (1968). We assumed that "rhyniophytes" such as *Cooksonia* (the oldest known vascular plant, Middle Silurian–Early Devonian) show ancestral conditions for vascular plants (dichotomous branching, protosteles usually referred to as centrarch but not showing clear differentiation of protoxylem and metaxylem, and terminal sporangia); this assumption is supported both by stratigraphy and by outgroup comparison with bryophytes (cf. Mishler & Churchill, 1984). On this basis, two major subgroups can be recognized among higher vascular plants. One consists of the Early Devonian zosterophylls and the lycopsids, united by exarch steles and lateral sporangia with transverse dehiscence. Lycopsids themselves are united by additional advances (microphylls, axillary or adaxial sporangia, actinosteles). The other major subgroup consists of the so-called trimerophytes (e.g., *Psilophyton*), ferns, sphenopsids, and lignophytes, which are united by elongate terminal sporangia with longitudinal dehiscence, mesarch or centrarch steles, and a strong tendency for differentiation of lateral branches (converted in various ways into leaves in higher groups) and a main trunk (overtopping).

Cladoxylales (a presumably paraphyletic group of Middle Devonian to Early Carboniferous age), primitive ferns, sphenopsids, and lignophytes are united by additional advances over trimerophytes: actinosteles and derived stelar types, and several mesarch protoxylem points. In addition, all living members (except for higher seed plants with nonmotile sperm) have multiflagellate sperm, an apparent advance over the biflagellate sperm of green algae, bryophytes, and lycopsids (except *Isoëtes*, presumably a convergence within lycopsids). Gensel (1984) has recently described an Early Devonian trimerophyte-like plant with a mesarch actinostele that may be the most primitive known member of this group. Cladoxylales, primitive ferns, and sphenopsids have at least one potential synapomorphy suggesting that they form a monophyletic group: presence of parenchyma in the protoxylem, resulting in "peripheral loops" of metaxylem, assuming that this condition is a step on the way to the characteristic protoxylem canals of sphenopsids and that its absence in more advanced ferns is due to secondary loss. However, since these assumptions are debatable (cf. Scheckler, 1974), we have treated Cladoxylales, sphenopsids, ferns, and lignophytes as an unresolved polychotomy. Ferns are

Table II

Data matrix used in this study, with terminal taxa (see Table I for abbreviations) scored for 62 binary characters (see **Appendices I** and **II** for detailed definitions). 0 designates the ancestral state, 1 the derived state. Different kinds of missing information are represented by the following symbols (all coded the same for computer analysis): — for relevant structure unknown; ? for structure known but character state uncertain; # for not applicable (structure not present in the group in question); X for precursor state unknown

	An	Ar	ML	HL	Md	Ca	Gl	Pl	Cs	Ct	Cy	Bn	Pn	Cd	Go	Cn	Ep	We	Gn	Ag
1 Axillary branching	0	0	?	1	1	1	1	—	—	1	?	1	1	1	1	1	1	1	1	1
2 Accessory buds	#	1	?	0	0	0	0	—	—	0	#	0	0	0	0	0	1	1	1	0
3 Penult. order leaves	0	0	0	0	0	0	X	0	0	0	X	X	X	1	1	1	X	X	X	X
4 Opposite leaves	0		0	0	0	0	0	—	0	0	0	0	0	0	0	0	1	1	1	0
5 Pinn. comp. leaves	0	0	1	1	1	1	1	1	1	1	1	1	1	1	X	X	X	X	1	1
6 Once-pinnate leaves	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	X	X	1	1
7 Linear-dichot. leaves	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
8 Non-bifurcate rachis	#	#	0	0	0	1	X	1	0	X	X	X	X	X	X	X	X	X	X	X
9 Reticulate venation	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1
10 >1 vein order	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
11 Flat guard cell poles	—	—	0	0	0	—	—	?	0	1	0	0	0	0	0	0	0	0	0	1
12 Syndetocheilic	—	—	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
13 Tunica-corpus	—	—	—	—	—	—	—	—	0	—	—	—	0	0	1	0	1	1		
14 Normal eustele	0	1	0	0	X	1	1	—	X	—	1	1	X	1	1	1	1	1	1	1
15 *Medullosa*-type stele	0	0	0	0	1	0	0	—	1	—	0	0	1	0	0	0	0	0	0	0
16 Endarch	0	0	0	0	0	0	—	—	0	—	1	1	?	0	1	1	1	1	1	1
17 Multilacunar node	0	0	0	0	1	0	—	—	1	—	1	0	X	0	X	0	X	X	1	1
18 2-trace node	0	0	0	0	0	0	—	—	0	—	0	0	1	0	1	0	1	1	0	0
19 CB meta- & protox.	0	0	0	0	0	0	0	—	0	—	0	0	0	0	1	1	1	1	1	0
20 Scalariform 2° xylem	0	0	0	0	0	0	0	—	0	—	0	1	1	0	0	0	0	0	X	1
21 Vessels	0	0	0	0	0	0	0	—	0	—	0	0	0	0	0	0	1	1	1	X
22 Multiseriate rays	0	0	1	1	1	1	0	—	0	—	1	1	1	0	0	0	1	1	1	1
23 Secretory canals	0	?	0	0	1	0	X	—	0	—	1	0	0	0	1	0	1	0	0	0
24 Mäule reaction	—	—	—	—	—	—	—	—	—	—	0	—	—	—	0	0	1	1	1	1
25 Pinn. comp. Msph.	0	0	0	1	1	1	X	1	1	1	1	X	X	X	X	X	X	X	X	1
26 Once-pinn. Msph.	0	0	0	0	0	0	X	1	0	1	X	X	X	0	0	0	X	X	X	1
27 One-veined Msph.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0
28 Pinn. comp. Msph.	0	0	0	1	1	1	X	1	1	1	1	1	0	X	X	X	X	X	X	1
29 Once-pinn. msph.	0	0	0	0	0	0	X	0	1	0	X	1	1	0	0	0	X	X	X	1
30 One-veined msph.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
31 Terminal ovule	#	#	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
32 FBs on last order	0	1	0	0	0	0	0	0	0	0	X	X	X	1	1	1	1	X	X	X
33 Loss of cupule	0	0	0	0	1	1	X	1	1	1	1	0	0	X	X	X	X	X	X	1

Table II
Continued

|	An	Ar	ML	HL	Md	Ca	Gl	Pl	Cs	Ct	Cy	Bn	Pn	Cd	Go	Cn	Ep	We	Gn	Ag
34 Anatropous cupule	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1
35 Second integument	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
36 1 ovule/anat. cupule	#	#	X	X	X	0	0	0	1	0	X	X	X	X	X	X	X	X	X	1
37 Abaxial msporangia	0	0	0	0	0	1	0	1	1	X	1	0	0	0	X	1	0	0	0	X
38 Microsynangia	0	0	1	1	1	1	0	0	0	1	0	1	X	0	0	0	1	1	X	1
39 Whorled msporoph.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0
40 Compound strobili	0	0	#	#	#	#	#	#	#	#	#	0	0	1	0	0	1	1	1	0
41 Radiospermic seeds	0	0	1	1	1	X	X	X	X	X	1	X	X	X	X	X	X	X	1	X
42 Platyspermic seeds	0	0	0	0	0	1	1	1	1	1	0	X	1	1	1	1	1	1	0	X
43 Lagenostome	0	0	1	1	1	1	X	1	1	1	X	X	X	X	X	X	X	X	X	X
44 Pollen chamber	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	X
45 Micropylar tube	0	0	0	0	0	0	X	X	0	0	1	0	0	0	0	0	1	1	1	0
46 Nucellar vasculature	—	—	0	0	1	0	0	—	—	0	1	0	0	X	0	0	0	0	0	0
47 Thick nuc. cuticle	#	#	?	?	?	?	1	0	0	1	0	X	1	?	0	0	0	0	0	1
48 Heterospory	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
49 Sulcus, pollen tube	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1
50 Tube, no sulcus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
51 Bilateral pollen	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1
52 Saccate pollen	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0	0	0
53 Granular exine	0	0	X	X	0	0	0	?	?	0	0	1	—	0	0	0	1	1	1	1
54 Striate pollen	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
55 Linear Mspore tetrad	0	0	0	0	?	—	—	—	—	—	1	1	—	—	1	1	1	#	#	1
56 Reduced Mspore wall	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	1	1	1
57 4-nucleate microgpt.	—	—	—	—	0	—	—	—	—	0	—	—	—	0	0	0	0	1	1	X
58 Siphonogamy	0	0	0	0	?	—	—	—	—	0	—	—	—	0	0	1	1	1	1	1
59 Tetrasporic megagpt.	0	0	0	—	—	—	—	—	—	0	0	—	—	—	0	0	0	1	1	0
60 Free-nuclear egg	#	#	0	0	0	0	—	—	—	0	0	—	—	0	0	0	0	1	1	0
61 Cellular embryogeny	—	—	—	—	—	—	—	—	—	0	—	—	—	0	0	0	1	1	1	
62 Feeder in embryo	—	—	—	—	—	—	—	—	—	0	—	—	—	0	0	0	1	1	0	

[a] M = mega
[b] m = micro
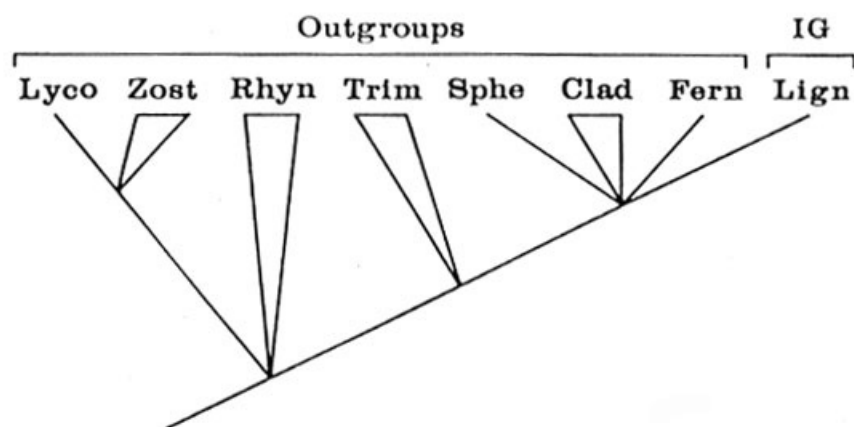
Fig. 1. Preliminary cladistic analysis of relationships of seed plants plus progymnosperms (lignophytes: the ingroup, IG) to other major groups of vascular plants (lycopsids, zosterophylls, rhyniopsids, trimerophytes, sphenopsids, Cladoxylales, and ferns: outgroups). Zosterophylls, rhyniopsids, trimerophytes, and Cladoxylales may be paraphyletic.

united by conversion of branch systems into pteridophylls, apparently via intermediates with a quadriseriate arrangement of pinnae or their homologs, as in *Arachnoxylon, Rhacophyton,* Zygopteridaceae, and *Stauropteris*. Sphenopsids are united by a shift to a whorled arrangement of the ultimate dichotomous branchlets and their transformation into well-defined sphenophylls and sporangiophores. It should be noted that this analysis differs from the once widespread view that ferns are the closest relatives of seed plants, recently reflected in a summary cladogram of green plants presented by Bremer (1985). Bremer links seed plants with ferns on possession of pinnate leaves and trichomes, but these characters are highly questionable as synapomorphies. Plesiomorphic fossil members of the cladoxylalian-sphenopsid-fern-lignophyte clade, including some linked with ferns (those with quadriseriate organization) and some linked with seed plants (progymnosperms) have three-dimensional branch systems rather than fronds, and trichomes are rare in gymnosperms other than cycads.

Even the most primitive lignophytes have several additional advances over other trimerophyte derivatives, supporting their monophyletic status: a bifacial cambium producing both secondary xylem and phloem, periderm produced by a cork cambium, cortical fiber strands (retained by many seed ferns and cordaites but apparently lost in more advanced groups), sterile branch systems with more or less regular repetition of the same pattern of pseudomonopodial branching, and differentiation of simple, dichotomous sterile appendages (leaves) and more complex dichot-

omous fertile appendages bearing groups of sporangia. Living seed plants have several other advances in organs that are not preserved in progymnosperms, such as several apical cells, loss of neck canal cells in the archegonium, a free nuclear stage in early embryogenesis, and an embryo with shoot apex, root apex, and suspensor in a line. In the absence of information on progymnosperms and extinct gymnosperms, it cannot be determined whether these are synapomorphies of all seed plants, of living groups only, or of lignophytes as a whole.

This analysis indicates either that the first outgroup to the lignophytes is Cladoxylales, sphenopsids, and ferns (if these form a monophyletic group), in which case trimerophytes are the second outgroup, or that the first two or more outgroups are some combination of Cladoxylales, sphenopsids, and ferns (if these form a paraphyletic group). Under either assumption, outgroup comparison indicates that *Aneurophyton* retains the ancestral state for lignophytes as a whole in all characters considered; hence it can be used as a functional first outgroup for assessment of polarities in the remaining taxa (the functional ingroup: Watrous & Wheeler, 1981). This conclusion is supported by the fact that the earliest lignophytes in the stratigraphic record are of the aneurophytalian type (*Protopteridium* from the Eifelian, predating *Svalbardia*, the oldest member of the Archaeopteridales, from the Givetian: Beck, 1976). Outgroup analysis (plus stratigraphy) also indicates that multiovulate lyginopterids are primitive in all characters relative to other seed ferns, allowing them to be used as a functional outgroup in assessing the polarity of characters such as bifurcation of the rachis and presence of a lagenostome.

On this basis, deciding on polarity and the resulting character coding was often unproblematical (e.g., homospory to heterospory, proximal to distal pollen germination, mesarch to endarch primary xylem). The greatest difficulties arose in coding multistate characters, where the ancestral state is clear but there are often different alternative interpretations of relationships of the several derived states to the ancestral state and to each other. In such cases, it is easy to bias the results by coding in a way that favors one pathway. We overcame this problem by devising a method of coding partially ordered characters that takes advantage of the algorithm's ability to deal with missing information in the data matrix. In order to illustrate this method and our general approach to character analysis, it is useful to discuss some of the most important examples in some detail. Other cases, most of which have close analogies to these, are discussed with the definitions of characters in Appendix II. It should be noted that our purpose was not to code every character so as to avoid all possible bias, which would allow no resolution of alternative phylogenetic hypotheses, but only those where there are major alternative morphological theories on homologies.

The first example concerns the presence and symmetry of seeds (character 41–42). Under the hypothesis that cycadopsids and coniferopsids evolved separately from progymnosperms (Beck, 1966, 1970, 1981; Meeuse, 1963), the radiospermic seeds of cycadopsids and the platyspermic seeds of coniferopsids both originated independently from no seeds. The platyspermic seeds of *Callistophyton* and other advanced seed ferns were still presumably derived secondarily from radiospermic ones within cycadopsids. Under the hypothesis that coniferopsids were derived from platyspermic seed ferns (Rothwell, 1982), the seed originated only once, the first seeds were radiospermic, and all platyspermic seeds were ultimately derived from radiospermic. Both ways of coding such a three-state character in standard binary form (Brooks, 1984) introduce undesirable biases (Fig. 2). Coding no seeds 00, radiospermic 10, and platyspermic 11 might be appropriate within seed ferns under either hypothesis, but it biases against the Beck hypothesis for the origin of coniferopsids by making the transition from no seeds to platyspermic a two-step change (both 0's in 00 must change to 1). This is essentially the coding used by Crane (1985a), since he codes presence of seeds as one advance and platyspermic as another. On the other hand, coding the three conditions 00, 10, and 01 adds an artifactual step to a direct transition from radiospermic to platyspermic (the 1 in 10 must change to 0, the 0 to 1), as required within cycadopsids under both hypotheses. Our solution was to code no seeds 00, radiospermic 10, and platyspermic X1 (i.e., either 01 or 11): platyspermic can thus be derived by one step from either no seeds (where the X is interpreted as 0) or radiospermic (where the X is interpreted as 1).

As we will discuss in detail elsewhere, this technique does introduce a subtle bias in some cases, by adding an extra step to a transition from no seeds to platyspermic to radiospermic. Basically, in such a series, the first 0 changes to 1 while the second 0 must change first to 1 and then back to 0. This means that the algorithm counts a total of three steps, when in reality only two changes need to have occurred. This bias occurs only with cladogram topologies where two or more groups with the X-coded state are positioned between groups with two different codings. There is no bias (i.e., only two steps are counted) whenever (1) the X-coded taxa form a clade, (2) when an X-coded taxon occurs by itself in the cladogram, or (3) when X-coded taxa are nested between two groups that have the same coding. In the case of the seed character, this bias is not likely to pose a problem, since there is no preliminary hypothesis of relationship or morphological evidence that implies that platyspermic groups were intermediate between progymnosperms and radiospermic seed ferns. In general, our primary concern was to avoid bias against hypotheses that have been proposed and that we wanted to test in our analysis, rather
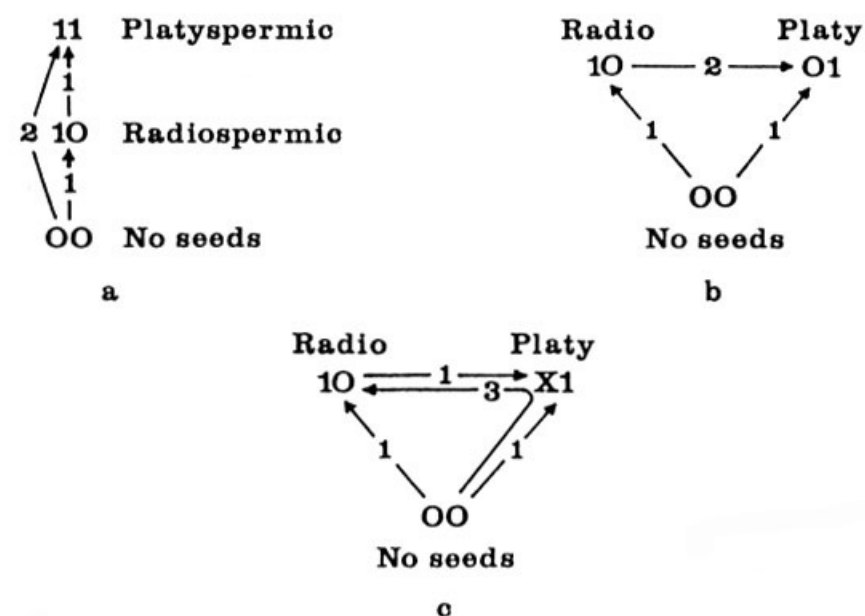

Fig. 2. (a, b) Standard alternative additive binary codings of a three-state character, presence and symmetry of seeds (character 41–42), and (c) the partially ordered coding used in this study, with numbers of steps between states indicated (see text for explanation).

than to allow for all conceivable possibilities. In any case, although trees with such extra steps will be rejected by the computer, all else being equal, alternative trees containing them can be manufactured using the methods discussed below, and the extra steps can be recognized and taken into account in discussion.

Our second example concerns major patterns of leaf architecture (character 5–7; Fig. 3). It is clear from outgroup comparison that branch systems with simple, dichotomously veined leaves (sphenophylls), as in progymnosperms, are ancestral in lignophytes, and both the Beck and Rothwell hypotheses interpret the fern-like pinnately compound fronds (pteridophylls) of seed ferns as derived from such branch systems, with the sphenophylls transformed into leaflets. Origin of pteridophylls seems to have been correlated with another change, the origin of scale-leaves or cataphylls. Cataphylls are reported in the Early Carboniferous seed fern *Pitus* (Gordon, 1935), and all other seed plants that are sufficiently known have them (if one includes the scale-like vegetative leaves of conifers). We envision two possible mechanisms for origin of cataphylls: differentiation from pteridophylls by truncation of development of regular vegetative leaf primordia (implicitly favored by Rothwell, 1982), or modification
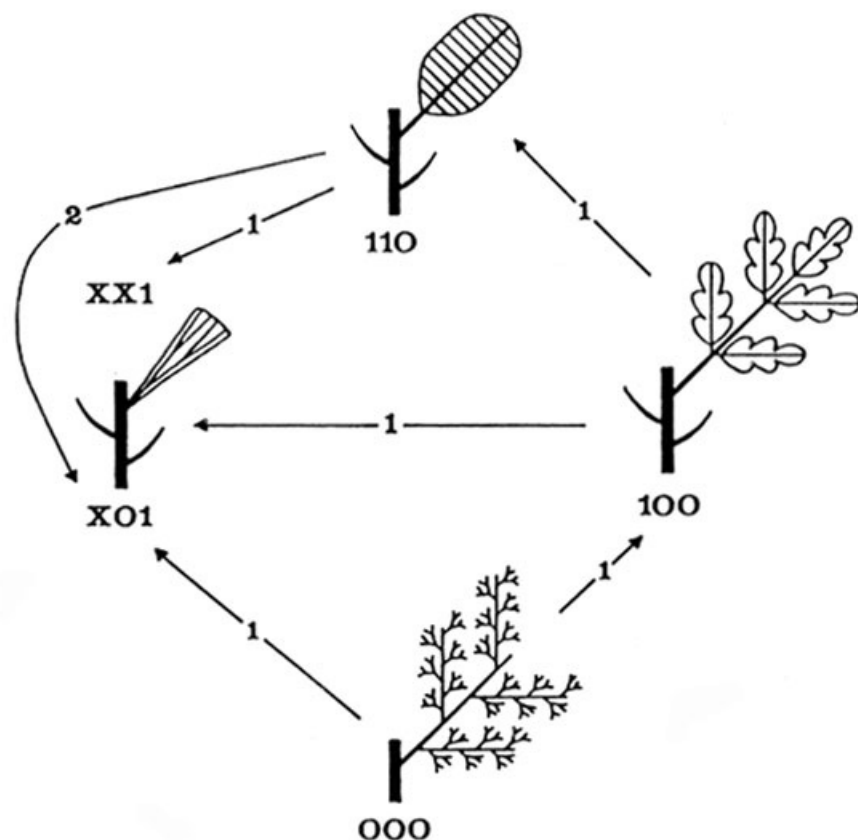
Fig. 3. Partially ordered coding of major patterns of leaf morphology used in this study (character 5–7), with numbers of steps between states indicated (see text for explanation).

of sphenophylls on lower-order axes that were never involved in the transformation of branch systems into pteridophylls. The former seems more likely, since in aneurophytes sphenophylls are known only on the last order axes, and although sphenophylls occur on the penultimate order axes and possible young plants of *Archaeopteris* (*Eddya*: Beck, 1967), most of its main axes apparently bore only branch systems (Beck, 1979). In keeping with Meyen's (1984) view that the whole spectrum of leaf types produced should be considered as a single complex character and in view of the tight correlation between the appearance of pteridophylls and cataphylls, we coded presence of both leaf types as 100, one step removed from 000. In medullosans, peltasperms, and corystosperms, where we found no information on cataphylls, we based scoring on the vegetative leaves.

Both comparison with the complex branch systems of progymnosperms and leaf architecture of primitive seed ferns clearly imply that several-times pinnately compound leaves are basic in cycadopsids. Hence it seems safe to interpret once-pinnate leaves of the cycad type as derived from fronds by simplification, so they are coded as 110. Under this category we also included simple leaves with a midrib and pinnate secondary venation, as in the form genus *Taeniopteris*. This is because both types occur in Bennettitales and cycads, some forms in both groups show intermediate degrees of dissection (e.g., *Nilssonia, Anomozamites*), and it is unclear which condition is ancestral. In Bennettitales, the oldest forms have dissected leaves, and taeniopterid leaves are best known in *Williamsoniella*, a supposedly advanced genus (Crane, 1985a). However, Mamay (1976) has suggested that cycads originally had undissected leaves, based on his interpretation of Permian taeniopterid leaves and megasporophylls as primitive cycads. Even if these are not accepted as cycads, taeniopterid leaves are common in Mesozoic cycads, and as Mamay also argues, *Cycas*- and *Zamia*-type leaves seem more easily derived from a taeniopterid prototype than from each other. In any case, the once-pinnate cycad type is more comparable to the taeniopterid type in overall venation than it is to the fronds of seed ferns, since the leaflets have parallel or dichotomizing venation in most cycads but are themselves pinnately organized in seed ferns. We also placed leaves of angiosperms and *Gnetum* in the 110 category, since their derivation from taeniopterid ancestors would involve no change in major venation, only origin of reticulations and interpolation of new vein orders (coded as characters 9 and 10), whereas derivation from pinnately compound would require at least one additional step, simplification.

More varied hypotheses have been proposed for the origin of the simple leaves of coniferopsids, which are one-veined or several-veined with parallel or dichotomous venation and no midrib. Under the Beck hypothesis, coniferopsid leaves are directly homologous with progymnosperm sphenophylls, while under the Rothwell hypothesis they are homologous with the cataphylls of seed ferns, pteridophylls having been eliminated by heterochrony. The coniferopsid leaf condition could also be derived by other mechanisms, such as reduction, phyllodization, or dedifferentiation (Meyen, 1984). The Beck hypothesis might seem at first to require no change in leaf architecture, since some coniferopsids (e.g., *Ginkgo*, some cordaites) have sphenophylls that are essentially like archaeopterid leaves. However, there actually is a change, since both ginkgos and cordaites have pointed cataphylls as well as sphenophylls (Rothwell, 1982). In order to avoid bias for or against either of these hypotheses, we coded the coniferopsid condition X01, which is one step removed from both progymnosperms and seed ferns. This represents a change from our pre-

vious study, in which coniferopsid leaves were coded XX1, which is also only one step from once-pinnate leaves of the cycad type (110, two steps from X01). It might be argued that XX1 is preferable, since under the heterochrony hypothesis it would seem just as plausible morphologically to derive coniferopsids from forms with cataphylls and once-pinnate leaves as from any other type. However, current theories do not relate coniferopsids most closely to plants with once-pinnate leaves, and derivation from such forms seems unlikely on stratigraphic grounds, since the first coniferopsids appear early in the Late Carboniferous, well before any groups with such leaves.

In order to allow for a broader range of possible prototypes, we did use XX1 to code the linear, parallel-veined leaves of *Ephedra* and *Welwitschia*. Although these leaves are difficult to separate from those of coniferopsids on similarity criteria (*Welwitschia* differs in having higher order cross-veins, but this is a separate character), there are current theories that postulate relationships of Gnetales with groups coded both X01 (coniferopsids) and 110 (Bennettitales, angiosperms), and plants with both sorts of leaves are widespread by the time Gnetales appear (possibly Triassic, surely Jurassic). With Gnetales coded XX1, no change occurs in character 5–7 if they are derived from coniferopsids.

As in the 110 category, there are major variations among the leaf types of coniferopsids, *Ephedra*, and *Welwitschia*, but we have not attempted to subdivide them at present. We considered coding the *Ginkgo* and cordaite condition, with a mixture of sphenophylls and cataphylls, as 010, which is two steps from the seed fern condition but one from progymnosperms, reasoning that derivation from seed ferns under the Rothwell hypothesis would require two steps (first loss of fronds, giving initially only cataphyll-like scale leaves, then secondary modification of some cataphylls to dichotomously veined leaves), while origin from progymnosperms would require only one step (differentiation of some leaves into cataphylls). However, putting two steps between seed ferns and cordaites would bias against other plausible scenarios: perhaps strap-shaped leaves were derived from fronds by one step, by phyllodization or a substitution of a "leaflet program" for a leaf one (cf. Meyen, 1984). Another reason to lump coniferopsid leaf types is that there are so many overlapping ways in which they can be categorized, depending on whether one stresses gross form (pointed in conifers and *Ephedra*; strap-shaped in cordaites and some ginkgos; fan-shaped in most ginkgos) or various aspects of venation (one-veined in most conifers; two-veined or multiveined and apically convergent in other conifers, *Ephedra*, and *Welwitschia*; multiveined and apically divergent in ginkgos and cordaites). Furthermore, conditions within groups are heterogeneous and the basic condition both within groups and in coniferopsids as a whole is unclear.

As in the seed character, it must be recognized that this system does introduce possible biases, by adding one or two steps when taxa with linear-dichotomous leaves (X01, XX1) are positioned between taxa with other states. The principal case where this might be anticipated is if *Gnetum*, coded 110, is directly or indirectly derived from (nested within) coniferopsids, which are in turn derived from ancestors coded 000 (progymnosperms) or 100 (seed ferns). Since *Ephedra* and *Welwitschia* have linear leaves, *Gnetum* leaves may have originated from linear precursors in any case (by secondary expansion and/or aggregation of veins into a midrib), but this does not involve any extra steps if Gnetales as a whole were derived from ancestors already coded 110, such as Bennettitales. This bias is not necessarily undesirable: it might be argued that it is easier from a developmental-genetic point of view to imagine reappearance of once-pinnate organization in a line that had once had it, perhaps by a regulatory mutation resulting in reactivation of a suppressed genetic program, than in a line where it had never existed, although arguments leading to contrary conclusions are also possible. In general, we used the X-coding to designate a reduced state, since it tends to inhibit some (though not all) kinds of trees that involve reduction and secondary elaboration of complex structures, which seems intuitively less likely than simple reduction.

Patterns closely analogous to those in leaf architecture are encountered in the morphology of the fertile appendages (25–30), where we used a similar system of coding, with certain modifications where character relationships are especially problematical (e.g., cycad sporophylls, glossopterid fructifications, angiosperm stamens: see **Appendix II**).

We used X-coding in a slightly different way in cases where one group has a unique condition (an autapomorphy) that may be logically derived either directly from the primitive condition or from a different derived condition seen in two or more other groups. A good example concerns the microgametophyte (57). The basic condition in seed plants appears to be presence of one or more prothallial cells plus a sterile cell (the sister cell of the spermatogenous cell). However, *Welwitschia* and *Gnetum* differ in having only one nucleus in addition to the tube and generative (spermatogenous) nuclei. Sterling (1963) argues that the third nucleus represents a sterile cell, mostly by analogy with the Cupressaceae and related conifer families, which have 3-nucleate microgametophytes with a sterile cell and no prothallials, whereas Martens (1971) argues on the basis of division sequences that it represents a prothallial cell. Under either interpretation, angiosperms are advanced over all other groups in lacking all but a tube and a generative nucleus, and we can see no way of determining whether they lost the other nuclei by passing through the gnetalian condition, simultaneously, or in another sequence. Coding *Welwitschia*

and *Gnetum* 10 and angiosperms 11 would bias in favor of the first pathway, while coding angiosperms 01 would bias in favor of the second or third. If more than one group had the angiosperm condition, an appropriate coding would be 10 for *Welwitschia* and *Gnetum* and X1 for the angiosperms, which would treat all three reduction pathways as equally likely. However, only angiosperms have the X1 state, making it an autapomorphy, and we have consistently eliminated autapomorphies from the matrix. This can be done by simplifying 00, 10, and X1 to 0, 1, and X. This simplification is entirely satisfactory, since as far as relationships with other groups are concerned, the two schemes convey the same information when only one group has the X state. The cupressaceous condition need not be coded, since there is little doubt that it is derived within conifers.

C. TYPES OF ANALYSIS

In the present study, we used two similar programs. In our initial analyses we used the Wagner parsimony algorithm in PHYSYS (Mickevich & Farris, 1982; Smith et al., 1982), run on the California State University Central Timesharing CDC CYBER 170 730/760 System. In later analyses, which included the rerunning of all the experiments described below, we used the Mixed Method Parsimony algorithm with the Wagner option in PHYLIP (Felsenstein, 1985), version 2.8, run on an Eagle PC microcomputer. Both algorithms are highly modified implementations of the Wagner parsimony method described by Kluge and Farris (1969) and Farris (1970). They begin with a matrix of taxa scored for binary characters and attempt to find the tree(s) that minimizes the total number of character state transitions (steps). They treat forward changes and reversals equally, a desirable feature in light of Meyen's (1984) criticisms of conventional botanical assumptions of irreversibility in plant evolution. With PHYSYS we regularly used two routines that are designed to improve chances of obtaining the most parsimonious tree(s), WAG.S for global branch-swapping, and PIM, which shuffles the order of entry of taxa, and with PHYLIP we used the less extensive "global" branch-swapping option. With PHYSYS, trees were rooted by specification of a hypothetical ancestor with 0's in all characters. With PHYLIP, trees were rooted by specifying *Aneurophyton* as outgroup to the rest. Inasmuch as *Aneurophyton* is primitive in all characters considered, the two rooting procedures give the same results.

In order to evaluate competing hypotheses on relationships, we generated alternative cladograms by adding "dummy" synapomorphies to the matrix to force particular groups together and then subtracted the corresponding numbers of extra steps after analysis. In analyses with

PHYLIP, we also employed the user tree option, which allows one to specify whole trees and determine their length. In principle, the dummy character technique should provide a "cleaner" test of competing hypotheses than the "user" option, since it focuses on the implications of different relationships among particular clades, while allowing the computer to determine the most parsimonious relationships within them and in other parts of the tree. This eliminates the confusing factor of potentially unparsimonious assumptions on relationships among groups that are not relevant to the question at hand. However, because of the problems in finding most parsimonious trees discussed below, we used both procedures. For example, we consistently user-specified trees with groups not directly involved in the experiment arranged as in the shortest trees. In addition to analyzing the entire data set, we performed several experimental analyses with various subsets of the data, as described in discussion of the results.

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. The PHYSYS algorithm used determines the order of entry based on an advancement index, but with PHYLIP the order of entry is specified by the user. Despite use of the global branch-swapping option, the shortest trees that we obtained with PHYSYS (124 steps) were found during use of the dummy character method described above. 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 using the user tree option. Additional most parsimonious trees were kindly brought to our attention by W. E. Stein (University of Michigan), who used the PAUP program of D. L. Swofford. 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 (for example, one 123-step tree was found with the order of entry An Ar ML HL Md Ca Gl Cd Cn Pl Cs Ct Ag Bn Pn Cy Go Ep We Gn). 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.

Placement of character state changes on cladograms produced by these algorithms is frequently ambiguous. Thus it may be equally parsimonious to assume that a derived state restricted to two adjacent groups arose independently or arose once and was reversed. PHYLIP indicates the

number of steps required in each character and whether changes must be assumed along each internode, thus leaving the exact placement of many changes to the user. PHYSYS treats forward changes and reversals as equally likely in computing trees, but when it places characters on the tree it prefers two origins over an origin and a loss. When faced with equally parsimonious alternatives, our policy was to assume two origins when a relatively complex structure is transformed into a simple one or is lost, but to assume an origin and a loss when the situation is reversed, following the assumption that it is easier to reduce or lose a complex structure than to elaborate one from a simple structure.

III. Most Parsimonious Trees

Altogether, we found 36 most parsimonious cladograms of 123 steps, which differ only in relatively inconsequential ways (reversing Bennettitales and *Pentoxylon* and/or variously rearranging *Callistophyton*, coniferopsids, corystosperms, and cycads). We will first consider one of these trees in detail (Fig. 4), and then discuss implications of the other arrangements. We have chosen to center the discussion on this tree, in part for convenience, in part because we find it somewhat more plausible than the others for reasons discussed below.

Arranged in pectinate fashion from the base are the progymnosperms *Aneurophyton* and *Archaeopteris*, two groups of Carboniferous lyginopterid seed ferns, the Late Carboniferous seed fern *Medullosa*, and a major clade that includes all of the extant groups of seed plants. *Aneurophyton* is primitive in all characters used, while *Archaeopteris* is united with seed plants on heterospory (character 48) and possibly phloem structure (Wight & Beck, 1984) but has three coniferopsid-like advances of its own (3, 14, 32). Seed plants form a monophyletic group, initially united by cataphylls and pinnately compound leaves (5), multiseriate rays (22), fused pollen sacs (38), and radiospermic seeds (41) with a lagenostome (43), all modified or reversed in some members. Axillary branching (1) may be another synapomorphy of seed plants, but this is uncertain: it is documented in *Lyginopteris* (Blanc-Louvel, 1966; Brenchley, 1913), but the mode of branching in multiovulate lyginopterids and *Heterangium* is unknown. The basal taxon within seed plants consists of the Early Carboniferous multiovulate lyginopterids, which retain aneurophyte-like protosteles and cupules on branch-like parts of a fertile frond. The next group, including the lyginopterids *Heterangium* (as reconstructed by Stewart, 1983) and *Lyginopteris*, is united with the remaining taxa in having fully planated fertile fronds (25, 28). *Lyginopteris* is also advanced over Early Carboniferous forms in having one ovule per cupule, but we omitted this character since it is not definitely established in *Heterangium*, and it is not known
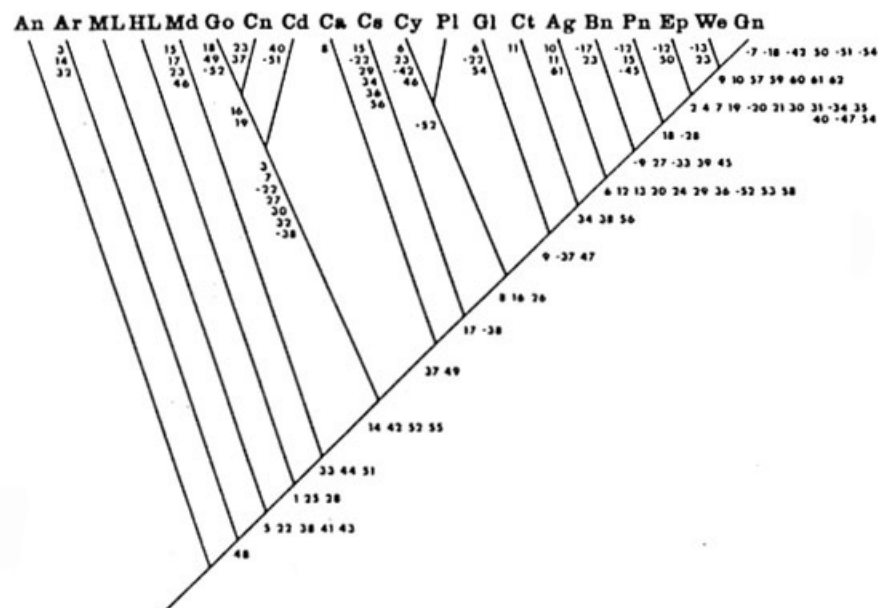

Fig. 4. Representative most parsimonious 123-step cladogram of progymnosperms and seed plants derived from analysis of the data matrix in **Table II**. Taxa are defined in **Table I** and **Appendix I**, characters in **Appendix II**. Minus signs before characters indicate reversals.

whether or not it existed in the ancestry of higher groups, which lack cupules of the lyginopterid type.

In Figure 4, *Medullosa* is the sister group of all remaining taxa, linked with higher seed plants on the basis of loss of the lyginopterid cupule (33), reduction of the lagenostome to a "normal" pollen chamber (44), and bilateral pollen (51). This contrasts with our previous scheme (Doyle & Donoghue, 1986), where the tree above lyginopterids splits into two major clades, derived from ancestors essentially identical to the Late Carboniferous seed ferns *Medullosa* and *Callistophyton*, respectively. In Figure 4, several typical "medullosan" features often considered evidence of relationships with cycads and/or corystosperms arise independently in these groups, such as a eustele with internal secondary wood (15), traces to each leaf derived from several vascular bundles or protoxylem areas around the stele (17, "multilacunar" nodes), secretory canals (23), and nucellar vasculature (46). These relationships are consistent with the hypothesis of Walton (1953) that the integument of medullosans and cycads (plus cordaites and conifers, according to Meyen, 1984) is actually a modified lyginopterid cupule, with the original integument reduced and represented only by the nucellar vasculature. However, they are also con-

sistent with loss of the cupule by reduction or dedifferentiation from the rest of the frond. Whichever hypothesis is correct, it presumably applies to all higher groups as well.

Excluding later reversals, the clade above *Medullosa* is united by normal eusteles (14), platyspermic seeds (42), and saccate pollen (52). Except for inclusion of cycads, it corresponds to the "platysperms" of Crane (1985b). A linear megaspore tetrad (55) may be another synapomorphy of this group, since it occurs in all members where the character is known, but it may have arisen at the previous node, since the condition in *Medullosa* is uncertain (see **Appendix II**). Another synapomorphy may be secretory cavities, which are known in *Callistophyton,* corystosperms, cordaites, and *Ginkgo*; we did not include this in the analysis because of uncertain homologies of secretory cavities and canals.

Exact relationships within the platyspermic clade shown in Figure 4 should not be taken too seriously, since equally parsimonious trees show many different arrangements of groups below glossopterids, many 124-step trees rearrange glossopterids and *Caytonia* as well, and information is lacking on many characters in several of these groups. The taxon that has retained the most primitive characters is the Late Carboniferous seed fern *Callistophyton.* It differs from the hypothetical ancestor of the clade only in having a non-bifurcate rachis (8, if the bifurcate rachis of corystosperms is a primitive retention), abaxial microsporangia (37), and a sulcus and pollen tube (49). Conifers, cordaites, and ginkgos form a group at the base of this clade, as in the scheme of Crane (1985a). They are united by simple leaves and sporophylls (7, 27, 30), secondarily uniseriate rays (22), secondarily free microsporangia (38), and patterns of leaf and sporophyll distribution comparable with *Archaeopteris* rather than *Aneurophyton* (3, 32). This result recalls the hypothesis of Rothwell (1982) that conifers were derived from *Callistophyton*-like platyspermic seed ferns with saccate pollen rather than *Archaeopteris*-like progymnosperms (Beck, 1971, 1981), but it implies that this concept should be extended to coniferopsids as a whole, as we have done. Coniferopsids thus appear to be a monophyletic group, but cycadopsids are paraphyletic (cf. Crane, 1985a, 1985b). Within coniferopsids, conifers and ginkgos are linked on strictly endarch primary xylem (16) and extension of circular bordered pits into the protoxylem (19); this differs from Crane's (1985a) scheme, in which conifers and cordaites are linked on possession of compound ovulate strobili (a character discussed further below). A sulcus and pollen tube (49) and abaxial microsporangia (37) arise independently within coniferopsids and at the *Callistophyton* node.

The position of conifers in our scheme might seem to conflict with Rothwell's (1982) concept that their pointed leaves are directly homologous with cataphylls of seed ferns, but this is not necessarily true; it is quite conceivable that the strap-shaped leaves of cordaites and the dichotomous leaves of ginkgos are separately derived from conifer-like leaves. The leaves of ginkgos are often considered primitive, but this does not follow outside the context of relationships with progymnosperms. The forked leaves on main axes of many Permo-Carboniferous conifers and the wedge-shaped, *Archaeopteris*-like leaves of the Permian genus *Buriadia* have also been considered primitive (Beck, 1971; Florin, 1951), but, as Rothwell (1982) notes, these groups (and ginkgos) are stratigraphically more recent than conifers with unforked leaves. In any case, if cataphylls originated as arrested frond primordia, it should not be surprising if their derivatives were sometimes forked, in view of the bifurcate rachis of early seed ferns.

In Figure 4, the remaining platyspermic groups, the more plesiomorphic of which are Permian and Mesozoic seed ferns and cycads, are initially united by multilacunar nodes (17, seen in cycads and corystosperms) and by secondarily free microsporangia (38), which arise independently in *Medullosa* and coniferopsids, respectively. The mesarch primary xylem of presumed stems of corystosperms (*Rhexoxylon*: Archangelsky, 1968) is apparently a primitive retention and their bifurcate rachis may also be, but their *Medullosa*-like internal secondary xylem (15) and multilacunar nodes (17) are convergences. It is most parsimonious to assume that multiseriate rays (22) independently reverse to uniseriate in corystosperms, glossopterids, and coniferopsids. Groups above corystosperms are united on a non-bifurcate rachis (8), endarch primary xylem (16), and once-pinnate megasporophylls (26). Unexpectedly, cycads are linked with the Permo-Triassic seed fern *Peltaspermum* (on secondary loss of saccate pollen, 52), not with medullosans as often suggested (although they are associated with *Medullosa* in other 123-step trees). With this arrangement, it is most parsimonious to assume that cycads are 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 (assumed to be secondary by Meyen, 1984). Furthermore, in several respects cycads resemble fossil platyspermic groups and/or other extant seed plants but are more advanced than *Medullosa,* such as endarch primary xylem, abaxial microsporangia, free pollen sacs, and pollen with a sulcus and pollen tube.

In agreement with Crane (1985a), the angiosperms, Bennettitales, *Pentoxylon,* and Gnetales form a monophyletic group within the platyspermic clade. This is a significant change from our previous analysis (Doyle & Donoghue, 1986), which linked these four taxa with medullosans and cycads. Since all four taxa show strong aggregation of sporophylls into flower-like structures, we will refer to them as the anthophyte clade. It may be objected that the term anthophyte is already in use as a synonym

for angiosperms, but we have deliberately extended it in order to emphasize the conclusion that flowers are not a unique advance of angiosperms but rather an older feature shared with related groups. The exact placement of the anthophytes differs in Crane's and our study: in all of our 123-step trees, the closest relatives of the anthophytes are *Caytonia* and glossopterids, whereas Crane (1985a) interpolated corystosperms between *Caytonia* and anthophytes (based on uniovulate cupules and granular exine structure, of which we do not consider the latter firmly established in corystosperms and thus coded as unknown). However, our scheme is consistent with Crane's proposed homology of the outer integument of angiosperms and the orthotropous cupules of Bennettitales and *Pentoxylon* with the reflexed cupules of Mesozoic seed ferns. These presumably represent enrolled leaflets bearing laminar ovules, since the original lyginopterid cupule was lost several nodes below. Glossopterids are linked with *Caytonia* and anthophytes on reticulate venation (9), which is later lost below Bennettitales, a shift away from abaxial microsporangia (37), and a thick nucellar cuticle (47). *Caytonia* is linked with anthophytes on anatropous cupules (34), presumably homologous with the cupules of glossopterids, secondary formation of microsynangia (38), and reduction of the megaspore wall (56). In our scheme, anatropous cupules and reduction of the megaspore wall originate independently in corystosperms and *Caytonia*, rather than being homologous.

Excluding later modifications, the anthophytes are united by presence of scalariform pitting in the secondary xylem (20), once-pinnate microsporophylls (29), one ovule per cupule (36), secondarily non-saccate pollen (52), granular exine structure (53), and possibly syndetocheilic stomata (12, assuming loss in *Pentoxylon* and *Ephedra*). We have shown leaves with simply pinnate organization (6) as originating independently in glossopterids and anthophytes, but it is equally parsimonious to assume that the simple leaf arose below glossopterids and the leaves of *Caytonia* are secondarily palmately compound; this unexpected possibility may be consistent with the presence of an abscission zone at the base of leaflets of *Caytonia* and their glossopterid-like appearance. Several characters that are not preserved in Bennettitales or *Pentoxylon* but occur in both angiosperms and Gnetales may be additional anthophyte synapomorphies: a tunica layer in the apical meristem (13), the Mäule reaction (24, an indication of lignin chemistry: Gibbs, 1957), and siphonogamy (58).

The exact arrangement of groups within the anthophytes also differs from Crane's (1985a) scheme, which groups angiosperms with Gnetales (as proposed by Arber & Parkin, 1908) on siphonogamy (which may actually be basic in anthophytes) and Bennettitales with *Pentoxylon*. Instead, our results imply that angiosperms are the sister group of the other anthophytes. Bennettitales, *Pentoxylon*, and Gnetales share several ad-

vances over angiosperms: erect, solitary ovules or cupules (27, 33), whorled microsporophylls (39), and possibly a micropylar tube (45), if the absence of this feature in *Pentoxylon* is due to loss. *Pentoxylon* is grouped with Gnetales on the presence of two-trace nodes (18), as in *Ephedra* and *Welwitschia*, and possibly secondarily three-dimensional microsporophylls (28); the latter may be an autapomorphy of *Pentoxylon*, but the fact that *Welwitschia* microsporophylls have three terminal pollen sacs suggests that they may have been derived from a *Pentoxylon*-like precursor. The three genera of Gnetales are in turn united by multiple axillary buds (2), opposite-decussate leaves (4), extension of circular bordered pits into the protoxylem (19), vessels (21), one-veined microsporophylls (30), a single terminal ovule (31), loss of the cupule (34), origin of a new outer integument from the perianth of the ovulate flower (35), compound strobili (40), and reduction of the thick nucellar cuticle (47). We interpret three features of *Ephedra* and *Welwitschia* as additional synapomorphies that were reversed in *Gnetum*: linear leaves (7), loss of scalariform secondary xylem pitting (20), and striate pollen (54), but it is equally parsimonious to assume that they arose separately in the two genera. Several of these features (linear leaves, pitting, reduced microsporophylls, compound strobili) represent convergences with coniferopsids. Within Gnetales, *Welwitschia* and *Gnetum* share additional advances over *Ephedra*, most of which represent convergences with angiosperms: vein anastomoses (9), interpolated higher-order veins (10), reduction of the male gametophyte (57), a tetrasporic megagametophyte with free nuclei serving as eggs (59, 60), cellular embryogeny (61), and a feeder in the embryo (62). Although Gnetales are thus the closest living relatives of angiosperms, most of the features commonly cited as evidence of relationship between the two groups (vessels, dicot-like leaves of *Gnetum*, simple stamens, embryology) arose independently, and most of the inferred homologies are rather cryptic (siphonogamy, tunica-corpus, lignin chemistry, reduced megaspore wall, granular exine). As we discuss elsewhere (Doyle & Donoghue, 1986), this goes far toward explaining why angiosperm-gnetalian relationships have been rejected by so many workers (including one of us: Doyle, 1978).

A. VARIATIONS AMONG MOST PARSIMONIOUS TREES

Differences between the tree in Figure 4 and other 123-step trees are summarized in Figure 5 (the tree in Fig. 4 is one of the variants in Fig. 5a).

With every topology found, it is equally parsimonious to reverse the order of Bennettitales and *Pentoxylon*, in which case Bennettitales are linked with Gnetales on possession of a micropylar tube, and the two-
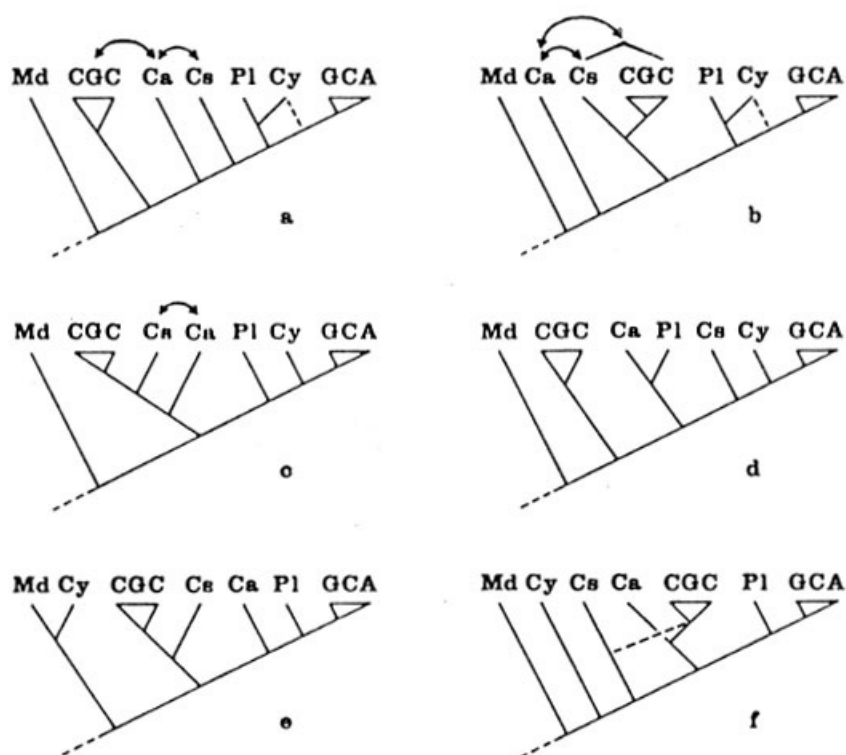
Fig. 5. Variations among the 36 most parsimonious 123-step cladograms, with equally parsimonious alternative positions of taxa indicated by double-headed arrows and dashed lines (note that in 5a and 5b, only one of the transpositions indicated among CGC, Ca, and Cs may be performed at once). CGC = conifers, ginkgos, and cordaites; GCA = glossopterids, *Caytonia*, and anthophytes. In all trees, groups below *Medullosa* are arranged as in Figure 4; groups in GCA may be arranged either as in Figure 4, or with Bennettitales and *Pentoxylon* reversed.

trace node originates twice. We find the arrangement in Figure 4 slightly preferable on stratigraphic grounds, since Bennettitales are known before *Pentoxylon* (Triassic vs. Jurassic).

Perhaps the most interesting variations involve alternative positions of cycads. In two trees, cycads are linked directly with *Medullosa*, as widely assumed (Fig. 5e). Here the commonly cited medullosan features of cycads, such as multilacunar nodes, mucilage canals, and nucellar vasculature, are homologies of the two groups. This arrangement may actually be slightly less parsimonious than it seems; because of the way we coded the stele character, the algorithm assumes that a regular eustele arose in the common ancestor of the *Medullosa*-cycad clade and other seed plants

and that the internal secondary xylem of *Medullosa* is an autapomorphy that never existed in the ancestry of cycads. However, there are in fact apparent protostelic relatives of *Medullosa* not included in our analysis (*Sutcliffia, Quaestora*) that suggest the eustele originated independently in the *Medullosa*-cycad clade and in platysperms, thus requiring two steps in the former clade. In other arrangements (Fig. 5f), cycads are the sister group of the platysperms. Here the multilacunar node is presumably basic in higher seed plants, but other typical "medullosan" features such as nucellar vasculature and secretory canals may have either originated below *Medullosa* and were later lost or modified in platysperms, or originated independently in *Medullosa* and cycads. Cycads are in turn linked with higher groups by a normal eustele, abaxial pollen sacs, and a sulcus and pollen tube. In other trees, cycads are interpolated between *Peltaspermum* and glossopterids (Fig. 5c–e, dashed lines in 5a and 5b); here simply pinnate leaves become a synapomorphy of cycads, glossopterids, and anthophytes that secondarily reverted to palmately compound in *Caytonia*, and non-saccate pollen must either arise independently in *Peltaspermum* and cycads or revert to saccate below glossopterids.

Other variants place corystosperms at the base of the platyspermic clade (e.g., Fig. 5b). In such trees, multilacunar nodes (and possibly a *Medullosa*-type eustele with internal secondary wood) are basic, and *Callistophyton* is linked with coniferopsids on reversion to unilacunar nodes. Other trees link corystosperms with coniferopsids (e.g., Fig. 5b, 5e), on secondarily free microsporangia and uniseriate rays. All of these trees are also somewhat implausible on stratigraphic grounds, since corystosperms are not known until the Triassic.

Some trees reverse the order of *Callistophyton* and coniferopsids (e.g., Fig. 5a), in which case secondarily free microsporangia are a synapomorphy of coniferopsids and higher groups.

An implausible aspect of many of these schemes, namely those with coniferopsids three or more nodes above *Medullosa* (e.g., Fig. 5c, 5f), is the fact that they imply that the terminal microsporangia and radial pollen of cordaites and the lack of a sulcus in cordaites and primitive conifers (Mapes & Rothwell, 1984), usually considered primitive characters, are secondary reversals.

In general, these variations among 123-step trees point up the instability of relationships around the *Medullosa*-cycad-platysperm nodes and the need for more data on morphological diversity of Paleozoic seed ferns. Many trees imply that there were other platyspermic seed ferns in the Carboniferous besides *Callistophyton*, including some with saccate pollen and medullosan anatomical features (particularly multilacunar nodes) that were eventually ancestral to corystosperms, *Caytonia*, and anthophytes. Reconstruction of additional Carboniferous platyspermic seed ferns, such

as *Lyrasperma*, associated by Meyen (1984) with *Stenomyelon*, and/or elucidation of the anatomy of the many Permian "peltasperms" and "callipterids" (Meyen, 1984) might help resolve these relationships.

B. GENERAL IMPLICATIONS OF MOST PARSIMONIOUS TREES

Inferences concerning major trends of evolution in leaf architecture and reproductive structures in seed plants are summarized in Figure 6. Considering vegetative features, our results imply that there was an iterative trend in seed plant evolution from a cycadopsid to a coniferopsid habit: from sparsely branched, manoxylic, and pinnate-leafed, to highly branched, pycnoxylic, and simple-leafed. This occurred first in the Carboniferous in platyspermic seed ferns, leading to coniferopsids, and then again in the Mesozoic in anthophytes, leading to Gnetales. Angiosperms themselves may represent a third, less extreme case. Both the Paleozoic and Mesozoic trends seem to have been associated with adaptation to drier habitats (cf. White, 1936). Other cases of inferred secondary origin of pycnoxylic anatomy (and less extreme but significant leaf simplification) are associated with geographic distributions indicating adaptation to temperate climates (glossopterids, corystosperms, *Pentoxylon*, possibly ginkgos).

Considering reproductive evolution within the anthophytes, we have already noted that flowers, derived by aggregation of originally pinnate mega- and microsporophylls of a seed fern type, were presumably an original feature of the clade, predating the origin of angiosperms. This contrasts sharply with both Wettstein's (1907) pseudanthial theory and more recent suggestions that flowers originated within the angiosperms (Dilcher, 1979; Krassilov, 1977; Meeuse, 1963, 1972a, 1972b; Meyen, 1984). Although the evidence is more equivocal, it is also possible that these flowers were bisexual and had a perianth, as assumed by Arber and Parkin (1907, 1908). Flowers of *Pentoxylon* are unisexual and the basic condition in Bennettitales is uncertain, but the presence of an abortive ovule in the staminate flower of *Welwitschia* suggests that Gnetales originally had bisexual flowers; a perianth is lacking in *Pentoxylon* and possibly some Bennettitales (*Vardekloeftia*: Harris, 1932b), but present in the other groups. As Arber and Parkin (1907) argued, angiosperms are primitive in retaining more complex megasporophylls but advanced in having highly simplified microsporophylls (with the two pairs of pollen sacs perhaps representing synangia of the *Caytonia* or bennettitalian type). Bennettitales are primitive in retaining pinnate microsporophylls, but pinnate megasporophylls were replaced by solitary ovules in the common ancestor of Bennettitales and Gnetales, presumably as a result of reduction of the megasporophylls. Gnetales went on to simplify the microsporophylls as well, independently of angiosperms, consistent with the idea
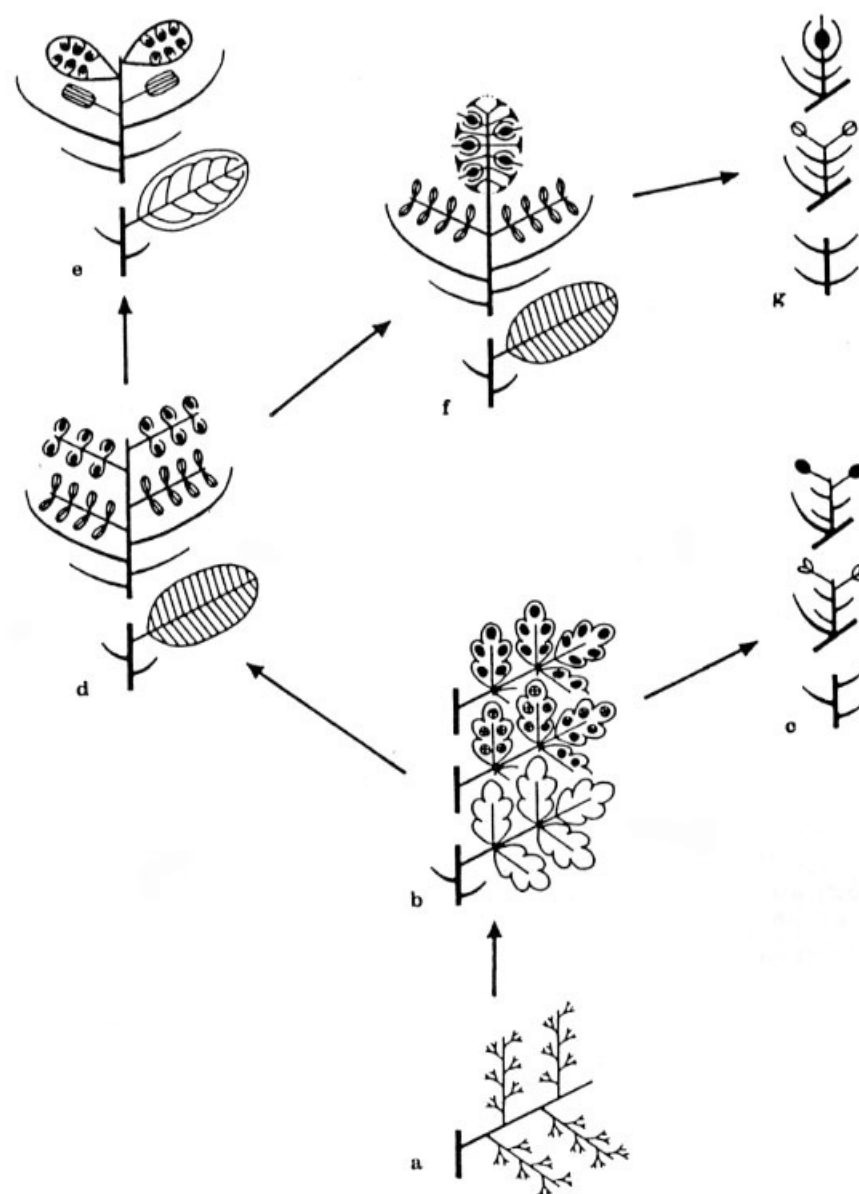
Fig. 6. Major transformations in leaf morphology and reproductive structures of seed plants inferred from the most parsimonious trees (Figs. 4 and 5), with emphasis on the anthophytes (angiosperms, Bennettitales, *Pentoxylon*, Gnetales). Groups indicated: (a) progymnosperms; (b) seed ferns; (c) primitive coniferopsids; (d) hypothetical common ancestor of anthophyes; (e) angiosperms; (f) Bennettitales; (g) Gnetales. See text for discussion.

that Gnetales are the product of a trend for drastic floral reduction and aggregation in response to wind pollination, like Amentiferae within angiosperms (Arber & Parkin, 1908).

In general, our results (and those of Crane, 1985a) go far toward bridging the gap between angiosperms and gymnosperms, since they imply that angiosperm flowers, carpels, and bitegmic ovules are structures with direct homologs in related groups. The same is true of the wood anatomy, stomatal structure, and granular monosulcate pollen of primitive angiosperms, all of which are essentially bennettitalian. The agreements with the ideas of Arber and Parkin (1907, 1908) are striking, but we stress that our results overcome many major weaknesses of their theory, since our results were derived from a much larger set of characters, many of which were not known to Arber and Parkin, and without their speculative assumption of a hypothetical ancestor with bisexual strobili. Arber and Parkin's scheme also left great morphological and stratigraphic gaps between anthophytes and other groups, since the closest relatives that they could identify were Paleozoic seed ferns. Much of this gap is filled by glossopterids and *Caytonia*, which have such anthophyte features as more simplified leaves and sporophylls, reflexed cupules potentially homologous with bitegmic ovules, detailed similarities in seed structure, and a sulcus and pollen tube.

By linking anthophytes with *Caytonia* and glossopterids, our results support the concept that the bitegmic ovule is a reflexed cupule (Crane, 1985a; Doyle, 1978; Gaussen, 1946; Retallack & Dilcher, 1981; Stebbins, 1974), but they still allow several interpretations of the origin of the carpel. Although we coded both *Caytonia* and angiosperms as having once-pinnate megasporophylls and glossopterids as potentially the same, their ovulate structures actually differ considerably in detail. Interpretations of their origin and subsequent modification may be placed in two main categories:

(1) That the common ancestor of glossopterids, *Caytonia*, and anthophytes had pinnate sporophylls, more or less like those of *Caytonia*, and that the glossopterid condition is an autapomorphic specialization. The latter might have arisen by fusion of a sporophyll to a leaf at a lower node (cf. epipetalous stamens in angiosperms), or by fusion of an axillary branch bearing a pinnate sporophyll to a subtending leaf. Here the angiosperm carpel most likely originated by expansion and folding of the sporophyll rachis, as suggested by Gaussen (1946), Stebbins (1974), and Doyle (1978).

(2) That the common ancestor had more glossopterid-like structures, with a blade-like portion and an adaxial fertile portion bearing several cupules. The idea that such structures were not restricted to glossopterids is enhanced by the recent report of an Early Cretaceous seed fern (*Ktalenia*: Taylor & Archangelsky, 1985) that had compound leaves with an adaxial segment bearing cupules and "bracts" (pinnules?). The fertile portion might represent an adaxially directed segment of a sporophyll, analogous to the adaxial fertile pinna of Ophioglossales; an adnate axillary branch bearing one pinnate sporophyll; or an axillary branch bearing several simple sporophylls. Under the first hypothesis, the *Caytonia* condition might have arisen by loss of the blade portion; under the latter two, the leaf and branch might have become intimately fused, or else the supposed megasporophylls of *Caytonia* may actually have been branches borne in the axil of a leaf. The angiosperm carpel could have originated either indirectly through a *Caytonia*-like structure by rachis expansion, or directly from a glossopterid structure by folding over of the blade-like portion, as proposed by Stebbins (1974) and Retallack and Dilcher (1981).

The solitary ovules of Bennettitales (and Gnetales) could be derived by reduction of any of these prototypes. Less plausible alternatives are that the bennettitalian ovuliferous receptacle is not an axis bearing reduced sporophylls but rather a secondarily terminal, radial sporophyll (as proposed for the whole bennettitalian flower by Delevoryas, 1968), or an adaxial fertile structure of the glossopterid type shifted to a terminal position.

Other problems, related to cupule orientation, are treated below, in the discussion of slightly less parsimonious cladograms.

IV. Problems and Experiments

Despite the attractive aspects of the schemes just presented, there are several reasons why they should be treated with caution. Most importantly, even our most parsimonious trees include a large amount of homoplasy: the existence of 123 steps for 62 binary characters means on the average one convergence or reversal per character (a consistency index, C, of 50.4). When homoplasy is common, many almost equally parsimonious arrangements can be expected, corresponding to different concepts of which shared advances are homologies and which are convergences. This is already evident from the many equally parsimonious arrangements of cycads and platyspermic groups. The results may also be unstable—sensitive to addition or deletion of taxa or characters or to minor changes in their interpretation (this is illustrated by another study in which we removed fossil groups from the matrix: Doyle & Donoghue, in press b). Furthermore, inspection of Figure 4 indicates that much of the homoplasy is associated with the evolution of those Mesozoic groups that we are most interested in (since we eliminated autapomorphies, all characters that change on the lines leading to terminal taxa must change elsewhere on the tree, and the amount of homoplasy in their origin may be estimated accordingly). By the Mesozoic, many of the early synapo-

morphies uniting major subgroups of lignophytes were becoming second-arily lost or obscured by subsequent modification in more advanced groups (e.g., symmetry of the reduced seeds of angiosperms and Bennettitales). In addition, geological evidence clearly documents general trends in Mesozoic environments (e.g., widespread monsoonal climate and aridity, increasing herbivore pressures) that might have favored convergent advances (e.g., leaf simplification, ovule protection, acceleration of the reproductive cycle).

Other problems concern the stratigraphic distribution of groups. In general, our results are gratifyingly consistent with the stratigraphic record, but they do conflict in some instances with known ranges. Sister lineages (though not necessarily all their apomorphies) should be of equal age. Thus, derivation of angiosperms and other anthophytes from a common ancestor indicates that the line leading to angiosperms existed at least as far back as the oldest known anthophytes (Late Triassic Bennettitales), but convincing angiosperm remains are not known until the Cretaceous. Similarly, as already noted, many 123-step trees (e.g., Fig. 5b, 5f) show coniferopsids nested among post-Carboniferous taxa, while they are actually the oldest well-documented platyspermic group (cordaites appear in the mid-Carboniferous). Our most parsimonious trees also require reversals that seem implausible on functional grounds, such as reversion of reticulate to open venation below Bennettitales; the fact that some Bennettitales (*Dictyozamites*) have reticulate venation might seem consistent with this scenario, but there is no indication from associated organs or stratigraphy that this feature is primitive in Bennettitales. Some trees also require secondary loss of the sulcus and pollen tube in coniferopsids. Such considerations are often discounted, since it is always possible that stratigraphic anomalies are due to gaps in the fossil record, and the plausibility of particular adaptive scenarios is often a function of the story-telling ability of the worker. However, others have argued that they can and should be used when faced with alternatives that are otherwise almost equally parsimonious (Doyle et al., 1982; Fisher, 1980, 1981).

A final cause for concern is that some supposed synapomorphies, especially in the anthophyte clade, are chemical, anatomical, and embryological features that are not preserved in most fossil groups. Perhaps information on the distribution of such characters in fossils would support alternative relationships. This is a special case of the general problem of inadvertent weighting of certain suites of characters.

These problems led us to undertake a series of computer experiments, designed to test the robustness of the results and the relative merits of alternatives, to identify areas that need more work, and to predict what sorts of paleobotanical discoveries might tend to confirm or refute particular hypotheses. The general result of these experiments is that several major parts of the tree appear to be quite stable (i.e., hard to break up without adding a large number of steps), but some of these clades can be placed almost equally parsimoniously in several different positions. Fortunately, one of the strongest groups appears to be the anthophyte clade.

A. RELATIONSHIPS OF MAJOR GROUPS OF SEED PLANTS

One experiment was to force coniferopsids together with *Archaeopteris*, as postulated under the Beck hypothesis. This resulted in trees only one step longer than our 123-step trees and otherwise the same in topology (Fig. 7a). These trees would eliminate the reversals and stratigraphic anomalies associated with some of the 123-step trees, but they would introduce another: the gap between the last occurrence of *Archaeopteris* (earliest Carboniferous) and the appearance of cordaites (Late Carboniferous). In fact, Rothwell (1982) cited this gap as evidence against the Beck hypothesis.

We conclude that although our results provide new support for the Rothwell hypothesis, the Beck hypothesis is still a highly viable alternative. Recognition of Carboniferous platyspermic seed ferns with more primitive pollen than *Callistophyton* and/or additional coniferopsid advances such as uniseriate rays or free microsporangia might shift the balance further in favor of the Rothwell hypothesis, while discovery of plants with a mixture of primitive progymnosperm-like features and coniferopsid advances (e.g., axillary branching and differentiation of cataphylls but no seeds, or progymnosperm-like branching and leaves but platyspermic seeds or saccate pollen) would support the Beck hypothesis. Incompletely known Early Carboniferous fossils that deserve attention in this context include *Archaeopteris*-like vegetative remains, such as *Rhacopteris* (Beck, 1970, 1971), and isolated platyspermic, lagenostomous seeds, such as *Lyrasperma*, which has been associated with protostelic calamopityan stems and assigned to the *Callistophyton*-peltasperm line (Meyen, 1984; Retallack, 1985).

Although we coded coniferopsid leaves so that they are not easily derived from pinnately veined simple leaves, some 124-step cladogram topologies discussed below place glossopterids directly below coniferopsids, raising the unexpected possibility that the simple glossopterid leaf type (except for its reticulate fine venation) represents an intermediate stage in reduction of a seed fern frond to a coniferopsid leaf (a different scenario from Rothwell's, which postulates heterochronic substitution of cataphylls for fronds). Alternatively, given this arrangement, the glossopterid leaf might be derived from an early parallel-dichotomous-veined coniferopsid type by aggregation of veins into a midrib; this would be consistent with the morphology of one glossopterid leaf genus, *Ganga-*
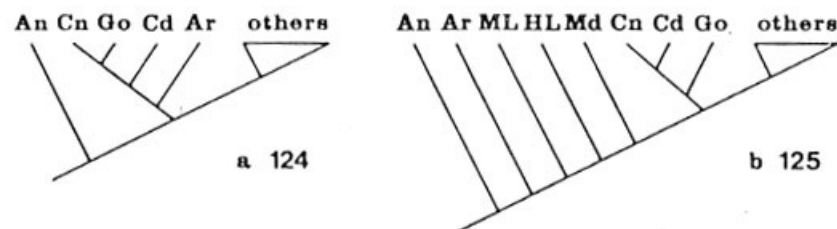
Fig. 7. Results of experiments designed to test alternative relationships of coniferopsids, with numbers of steps indicated next to trees. (a) One of several most parsimonious trees obtained with coniferopsids forced together with *Archaeopteris*, as in the "Beck" hypothesis. (b) Most parsimonious tree with ginkgos rather than cordaites basal in coniferopsids. Taxa not indicated are arranged as in Figure 4.

mopteris, which has no distinct midrib (cf. Schopf, 1976). If these relationships are correct, glossopterid fructifications might best be interpreted as homologous with the bract-fertile shoot complex of coniferopsids; i.e., as consisting of a leaf with an adnate axillary branch bearing one or more simple sporophylls.

Considering relationships within coniferopsids, an alternative that deserves attention is that ginkgos are basal in coniferopsids, as in the scheme of Crane (1985a). Two potentially ancestral features of ginkgos that might seem to favor a basal position are fan-shaped leaves and non-saccate pollen. However, this arrangement is two steps less parsimonious than that with cordaites basal (Fig. 7b). This result should not be surprising, since, as we have noted, dichotomous leaves and non-saccate pollen are more likely advances if coniferopsids are related to saccate seed ferns. Unexpectedly, the same difference in parsimony is found between the two arrangements in Beck-type trees, where coniferopsids are linked with *Archaeopteris*, despite the fact that *Archaeopteris* lacked saccate pollen. One obvious potential synapomorphy of conifers and cordaites that would favor a basal position of ginkgos is the presence of compound female strobili. Since this character was emphasized by Florin (1951) and used as a synapomorphy by Crane (1985a), it may be asked why we did not include it as a character. Basically, we accept Florin's proposed homologies between the parts making up these structures, but we question whether their aggregation into compound strobili is homologous. These doubts are based on the different plan of the female strobili in the two groups (four-ranked in cordaites and spiral in conifers) and the fact that the male compound strobili of cordaites are constructed on the same plan as the female strobili, whereas the male cones in conifers are on normal branches (**Appendix II**); together, these observations suggest that reproductive structures followed separate pathways of aggregation in the two groups. Some extant species of *Podocarpus* have compound male strobili that

have been considered primitive in conifers and evidence of a direct conifer-cordaite relationship (Wilde, 1944); however, based on the morphology of Carboniferous conifers, we assume that the podocarp condition is derived within conifers.

Other experiments were designed to assess Meyen's (1984) views on seed plant phylogeny. Very unparsimonious results (Fig. 8a: 150 steps) were obtained when seed plant taxa were forced into two groups according to his hypothesis that *Callistophyton*, peltasperms, glossopterids, ginkgos, *Pentoxylon*, and *Ephedra* form a primarily platyspermic line (ginkgoopsids) distinct from the radiospermic lyginopterids, medullosans, cycads, Bennettitales, *Welwitschia*, *Gnetum*, and angiosperms (cycadopsids) and the secondarily platyspermic conifers and cordaites (pinopsids). Curiously, the pinopsids and a group consisting of ginkgos, *Pentoxylon*, and *Ephedra* are basal in the two resulting seed plant clades, which conflicts with Meyen's concept that pinopsids underwent the same transformation of the lyginopterid cupule into a new integument as inferred in medullosans, and that ginkgos are closely related to peltasperms; two extra steps are required to move either group higher in its respective clade. We conclude that it is far better to assume that the platyspermic groups (and higher "cycadopsids") form a single clade than it is to divide them into two separate lines, each of which includes taxa with close analogs in the other line (ginkgos vs. coniferopsids, *Caytonia* and glossopterids vs. angiosperms, *Pentoxylon* vs. Bennettitales, *Ephedra* vs. *Welwitschia* and *Gnetum*).

On the other hand, our results suggest that Meyen's (1984) ideas on the position of ginkgophytes deserve further attention. The shortest tree found when ginkgos were forced together with *Peltaspermum* (Fig. 8b) is five steps longer than the shortest trees, but the real difference in parsimony may be less than the count of steps indicates, since it seems in retrospect that the strength of the linkage of ginkgos with conifers and cordaites may have been exaggerated by our definition of characters. Two of the characters uniting coniferopsids (3, 32) express *Archaeopteris*-like habital features that are less meaningful in a seed fern context (they might be expected as automatic consequences of the reorganization of branching patterns required in derivation of coniferopsids from seed ferns), and three might be the result of a single developmental change (reduction of leaves, megasporophylls, and microsporophylls).

Future observations on missing characters in peltasperms might further strengthen peltasperm-ginkgo relationships. For example, one possible synapomorphy of the two groups mentioned by Meyen (1984) is presence of two-trace nodes: this feature is not demonstrated in *Peltaspermum*, but compression fossils seem to show two bundles in the petiole, suggesting that it may have been present. Addition of Permian peltasperm groups
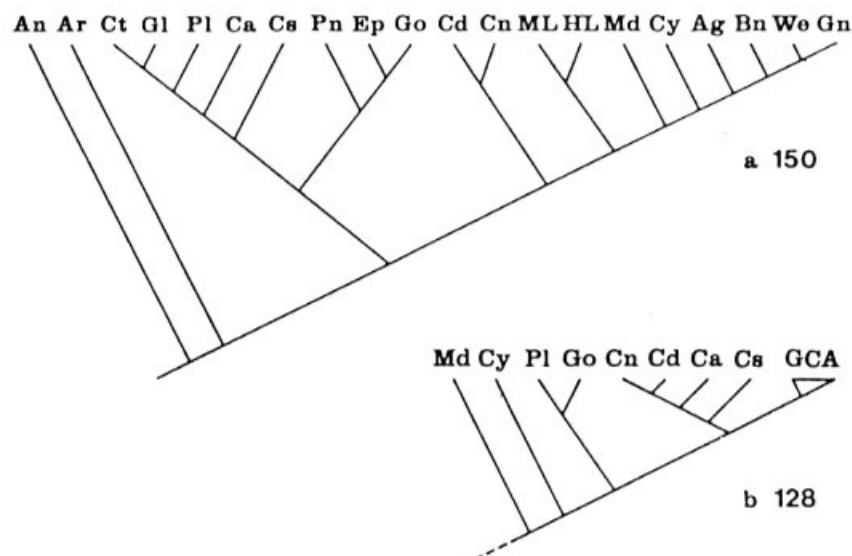
An Ar Ct Gl Pl Ca Cs Pn Ep Go Cd Cn ML HL Md Cy Ag Bn We Gn

a 150

Md Cy Pl Go Cn Cd Ca Cs GCA

b 128

Fig. 8. Experiments designed to test phylogenetic concepts of Meyen (1984), with numbers of steps indicated. (a) Most parsimonious tree obtained with seed plants forced into two clades corresponding to Meyen's Ginkgoopsida vs. Cycadopsida and Pinopsida. (b) Most parsimonious tree obtained with ginkgos forced together with *Peltaspermum*. GCA = glossopterids, *Caytonia*, and anthophytes; taxa not indicated are arranged as in Figure 4.

considered transitional to ginkgos by Meyen, which we did not include because of missing information on too many characters and because we were concentrating on the angiosperm problem, might also improve the parsimony of peltasperm-ginkgo relationships. For example, several of these groups have saccate pollen, which suggests that non-saccate, monosulcate pollen could be another synapomorphy of ginkgos and *Peltaspermum*. In Figure 8b, ginkgos and *Peltaspermum* form a clade below other platysperms, and their pollen is primitively non-saccate, but trees in which they are nested within the platysperms (in the position of *Peltaspermum* in Fig. 4) are only one step longer. In addition, since part of what associates ginkgos with coniferopsids is their specific anatomical similarities with conifers, new evidence for a direct link between conifers and cordaites might also have the effect of dissociating ginkgos from coniferopsids entirely and associating them with peltasperms.

B. POSITION AND UNITY OF THE ANTHOPHYTE CLADE

Most of our experiments were designed to assess the position and the unity of the anthophyte clade. In general, these experiments show that

several alternative positions for the anthophytes are nearly as parsimonious as that shown in Figure 4, but several more steps are required to move one or another subgroup of anthophytes to an alternative position than to move anthophytes as a whole, thus demonstrating the robustness of the anthophytes as a natural group.

The most parsimonious position for anthophytes found in our previous study (Doyle & Donoghue, 1986) was linked to cycads and *Medullosa*. As a result of recoding the ovule, cupule, and cycad sporophyll characters, such trees are now three steps less parsimonious than the shortest trees (126 steps). One is identical to the tree figured in our previous study (Fig. 9a); in others, Gnetales are the sister group of angiosperms, Bennettitales, and *Pentoxylon* (Fig. 9b). In all these trees, simply pinnate leaves and sporophylls, a normal endarch eustele, and sulcate pollen are cycad-anthophyte synapomorphies, and cupules and a reduced megaspore wall originate independently in anthophytes and Mesozoic seed ferns; in trees of the second type, the lack of a cupule in Gnetales is a primitive feature rather than a loss. These trees may actually be slightly more parsimonious than the count of steps would imply, since one step, the shift to uniovulate anatropous cupules (character 36), is an artifact: with this arrangement, multiovulate anatropous cupules never existed in the ancestry of anthophytes. In contrast, trees in which Bennettitales, *Pentoxylon*, and Gnetales alone are associated with cycads and *Medullosa* while angiosperms remain with *Caytonia* and glossopterids (Fig. 9c) are another six steps longer (132 steps).

As we noted in our previous study, the arrangements in Figure 9a and 9b are less satisfying than those linking anthophytes with Mesozoic seed ferns, since they do not provide homologs for the anatropous bitegmic ovule of angiosperms and the cupule of Bennettitales and *Pentoxylon*. However, a related alternative that would avoid this difficulty is that both anthophytes and at least some Mesozoic seed ferns are related not to the platyspermic groups but to medullosans. This hypothesis has the disadvantage of implying that the saccate pollen and platyspermic ovules of Mesozoic seed ferns originated independently from those in other groups, but it would explain the fact that one Mesozoic seed fern group, corystosperms, appears to have stems with remarkably *Medullosa*-like anatomy (*Rhexoxylon*: Archangelsky, 1968), and small sacs are present in one presumed medullosan pollen type (*Parasporites*: Millay & Taylor, 1976). In fact, we found cladograms with *Caytonia* and corystosperms as well as anthophytes associated with *Medullosa* and cycads (Fig. 9d) that are only two steps longer than our shortest trees (125 steps); these trees show both orders of *Caytonia* and corystosperms and an arrangement linking angiosperms directly with *Caytonia*. Interestingly, cycads are linked directly with *Medullosa*, presumably because the similar leaves of cycads
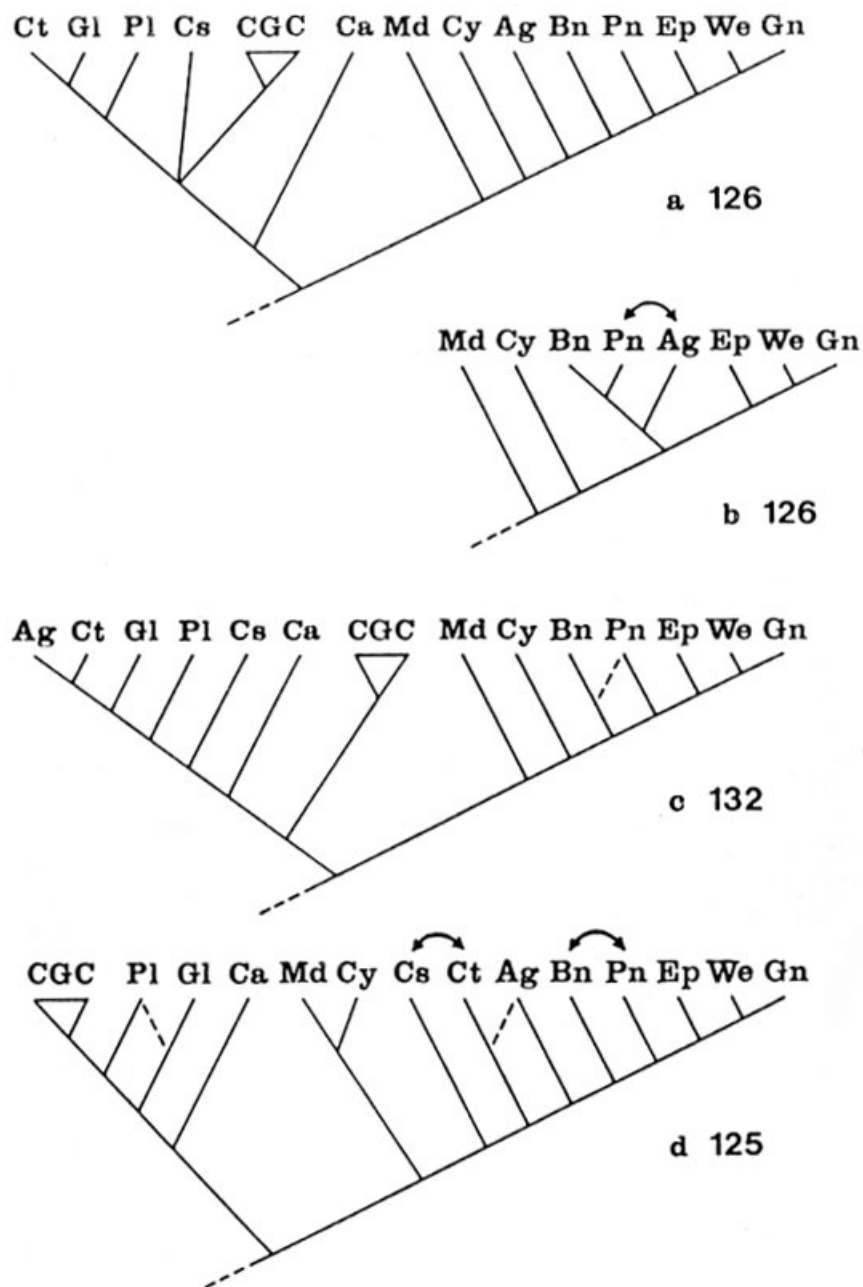
Fig. 9. Experiments associating angiosperms and/or putatively related groups with *Medullosa* and cycads, with numbers of steps indicated. Double-headed arrows and dashed lines indicate equally parsimonious alternative positions of groups. (a, b) Most parsimonious

and primitive anthophytes cannot be homologous when Mesozoic seed ferns are interpolated between them.

Another hypothesis worth considering is that anthophytes belong in a more basal position among seed plants, near lyginopterids. This would be consistent with a direct homology of the cupule of angiosperms, Bennettitales, and *Pentoxylon* with the lyginopterid cupule, an alternative considered by Crane (1985a), and the widespread notion that all but the most primitive seed ferns are too advanced to be angiosperm ancestors. It would also allow the granular monosulcate pollen of primitive angiosperms and other anthophytes to be derived directly from the nearly structureless trilete prepollen of lyginopterids (cf. Walker, 1976), rather than going through the coarsely alveolar saccate pollen type of lower platysperms, as implied by our most parsimonious trees. The shortest trees of this sort, with anthophytes interpolated between lyginopterids and *Medullosa* (Fig. 10), are only two steps less parsimonious than our shortest trees (125 steps). However, it should be noted that they are much less plausible from a stratigraphic point of view, since any common ancestor of *Medullosa* and anthophytes must be older than Late Carboniferous, while the first known anthophytes are Triassic. Furthermore, these trees require independent origin of advanced reproductive features shared with Mesozoic seed ferns, such as details of seed morphology, which we find less plausible than the concept that the resemblances in exine structure are convergent. Finally, Figure 10 implies either that a sulcus and pollen tube arose independently in anthophytes and the platyspermic groups, or that the absence of a sulcus in *Medullosa,* cordaites, and primitive conifers is due to secondary loss.

The least securely included group in the anthophytes appears to be the Gnetales, which can be moved to their widely suggested alternative position in the coniferopsids with addition of only four steps and no change in the topology of other groups (Fig. 11a, 127 steps). Interestingly, Gnetales are nested within coniferopsids as the sister group of ginkgos, based on their advanced primary xylem, two-trace nodes, and secondarily nonsaccate pollen. Thus, even if Gnetales are considered coniferopsids, the

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←
trees obtained with anthophytes forced together with *Medullosa* and cycads. (c) Two of several most parsimonious trees obtained with Bennettitales, *Pentoxylon,* and Gnetales forced together with *Medullosa* and cycads; position of angiosperms unconstrained. (d) Most parsimonious trees obtained with *Caytonia* and corystosperms also included in the *Medullosa*-cycad-anthophyte clade (note that only one of the transpositions indicated among Cs, Ct, and Ag may be performed at once, and that not all possible combinations of transpositions in different parts of the tree have been confirmed). CGC = conifers, ginkgos, and cordaites. Taxa not indicated are arranged as in Figure 4, except in 9b, where they are arranged as in 9a.
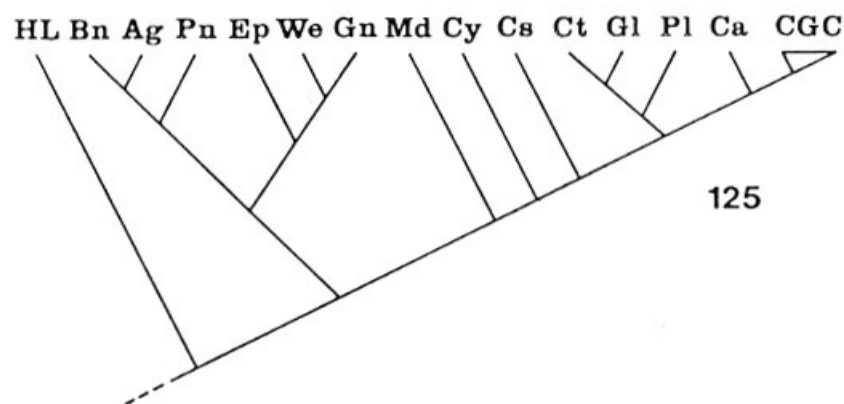
Fig. 10. Most parsimonious tree obtained with anthophytes forced below *Medullosa*, as under the hypothesis that the cupules of Bennettitales and *Pentoxylon* and the outer integument of angiosperms are homologous with cupules of lyginopterids. CGC = conifers, ginkgos, and cordaites; groups below HL are arranged as in Figure 4.

similarities between the compound strobili of *Ephedra* and cordaites emphasized by Eames (1952) are best interpreted as convergences. Another experiment strongly supports the concept that the three genera of Gnetales form a natural group, despite their conspicuous differences: forcing *Ephedra* into the coniferopsids and leaving *Welwitschia* and *Gnetum* associated with Bennettitales, as proposed by Eames (1952), adds 11 steps.

A more remarkable (and disconcerting) result is that a tree only two steps longer than our best trees (125 steps) can be obtained by moving anthophytes as a whole into the coniferopsids and rearranging other taxa somewhat (Fig. 11b). Here Gnetales are the sister group of angiosperms, *Pentoxylon,* and Bennettitales, consistent with the notion that the latter groups originated from coniferopsids via Gnetales-like intermediates, as envisioned for angiosperms by Wettstein (1907). It should be noted, however, that this tree would not support Wettstein's pseudanthial interpretation of the angiosperm flower, but rather one based on elaboration: it interpolates Bennettitales and *Pentoxylon* between Gnetales and angiosperms, and these groups have flowers with parts in the same arrangement as Gnetales, differing only in complexity. Actually, this "neo-englerian" arrangement is even shorter in terms of "real" steps, since one step, the shift to uniovulate cupules in angiosperms, is an artifact, and another is due to the fact that our coding puts two steps between no cupules (100) and erect cupules (010), so that the algorithm counts three steps in this character in the bennettitalian-*Pentoxylon*-angiosperm clade, whereas only two changes are really needed (origin of orthotropous cupules at the base of the clade, shift to anatropous in angiosperms). However, we find Figure
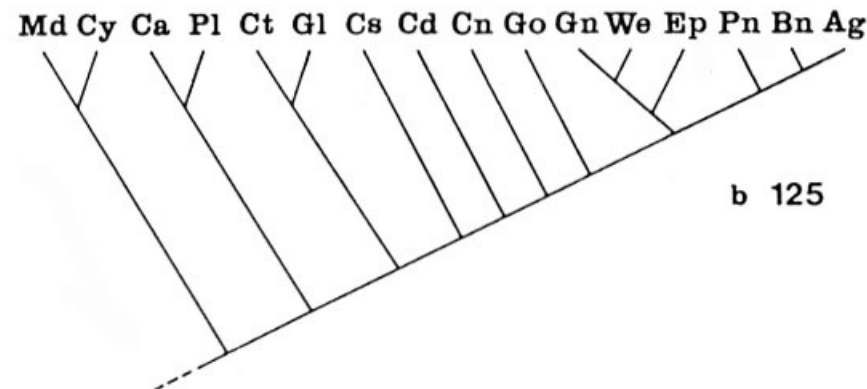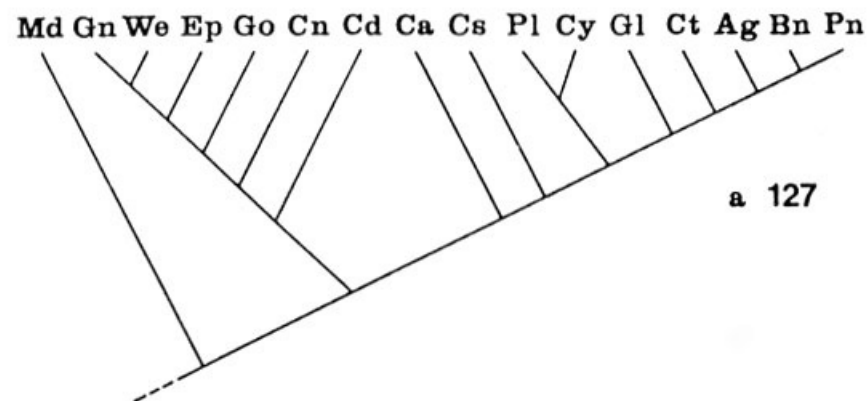
Fig. 11. Experiments relating Gnetales and anthophytes as a whole to coniferopsids, with numbers of steps indicated. (a) Most parsimonious tree obtained with Gnetales alone forced together with coniferopsids. (b) Most parsimonious tree obtained with anthophytes as a whole forced together with coniferopsids (a "neo-englerian" arrangement). Groups not indicated are arranged as in Figure 4.

11b much less plausible than the 123-step trees in morphological terms, since it requires first drastic reduction of leaves and sporophylls (to essentially nothing in the case of the megasporophylls of ginkgos and Gnetales), then re-elaboration of a more complex pinnate pattern convergent with that of Mesozoic seed ferns and cycads. This seems much harder to imagine than the alternative scenario, which interprets the similarities between the appendages of Gnetales and coniferopsids as due to independent reduction: reduction may be expected to give similar results whatever the starting point, but it seems less likely that elaboration of complex structures from simple ones would produce results similar to

those in other groups. Figure 11b also requires a shift from cycadopsid to coniferopsid anatomical features and back again and de novo origin of the cupule or outer integument.

These results show that earlier authors were right in seeing evidence for relationships between Gnetales and coniferopsids, but they indicate that the links between Gnetales and other anthophytes are stronger, so that if Gnetales are moved into the coniferopsids, it is most parsimonious to move the rest of the anthophytes with them. This is illustrated by re-examination of the organs cited as showing evidence for gnetalian-coniferopsid relationships. Like coniferopsids, Gnetales have reproductive structures consisting of bracts and axillary fertile shoots, but they have whorled microsporophylls with fused pollen sacs and ovules with a micropylar tube and a reduced megaspore wall, features anomalous in coniferopsids but typical of Bennettitales (and to some extent angiosperms and *Caytonia*). Similarly, although Gnetales resemble conifers and *Ginkgo* in having small tracheids and no scalariform pitting in the primary xylem, they are like cycadopsids in having multiseriate rays. The report of scalariform perforations in *Gnetum* (Muhammad & Sattler, 1982) is also consistent with anthophyte relationships.

The link between anthophytes and ginkgos in the neo-englerian tree recalls the suggestion of Krassilov (1977) that (some) angiosperms are derived from Mesozoic Czekanowskiales, since these are probably best interpreted as advanced ginkgophytes (Meyen, 1984). However, our results imply that this concept would be better extended to anthophytes as a whole. Even with this reformulation, closer examination shows additional difficulties not expressed in our character coding: unlike cordaites and primitive conifers, ginkgos lack sterile appendages on their axillary fertile shoots that might be homologized with a perianth.

The best alternative positions of the anthophytes were found in a variety of trees only one step longer (124 steps) than our shortest trees. Most of these also differ from Figure 4 in placing cycads as the sister group of the platyspermic clade and nesting coniferopsids well within the platysperms. One example is shown in Figure 12a. Here, as in some 123-step trees, all higher seed plants may be derived from *Medullosa*-like ancestors. Above cycads, the platyspermic groups split into two major clades. One, which includes *Callistophyton* and coniferopsids, is united by reversion to unilacunar nodes (a retained ancestral trait in Fig. 4) and a non-bifurcate rachis. *Peltaspermum* and glossopterids are interpolated between *Callistophyton* and coniferopsids, based on the secondarily free microsporangia of both groups and the uniseriate rays of glossopterids. Like some of our 123-step trees, this scheme has the implausible feature of implying that the terminal microsporangia and radial pollen of cordaites and the lack of a sulcus in cordaites and primitive conifers are secondary reversals.
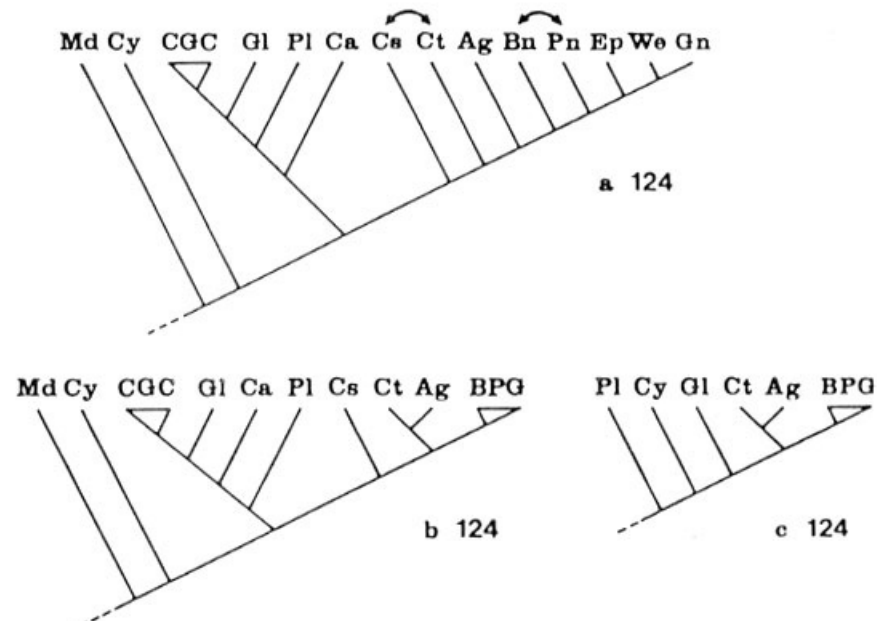

Fig. 12. Representative 124-step trees. Double-headed arrows indicate equally parsimonious alternative arrangements of taxa. (a) Trees with anthophytes linked with corystosperms and *Caytonia*. (b, c) Trees with angiosperms linked directly with *Caytonia*. CGC = conifers, ginkgos, and cordaites; BPG = Bennettitales, *Pentoxylon*, and Gnetales. Groups not indicated are arranged as in Figure 4.

The other clade, which consists of corystosperms, *Caytonia*, and anthophytes, is united by anatropous cupules and reduction of the megaspore wall, both of which arise twice in our 123-step trees. Some medullosan features of this clade (bifurcate rachis, multilacunar nodes) may be primitive retentions, but the internal secondary xylem of corystosperms is best interpreted as independently derived. *Caytonia* is linked with anthophytes by once-pinnate megasporophylls and a thick nucellar cuticle. It is equally parsimonious to assume that reticulate venation originated below *Caytonia* and was lost below Bennettitales, or that it originated independently in *Caytonia* and angiosperms.

As in the 123-step trees, it is equally parsimonious to reverse Bennettitales and *Pentoxylon*. Other 124-step trees (arrow in Fig. 12a) reverse the order of corystosperms and *Caytonia*; here once-pinnate microsporophylls and uniovulate cupules are synapomorphies of corystosperms and anthophytes (as in Crane, 1985a), and once-pinnate megasporophylls and a thick nucellar cuticle originate independently in *Caytonia* and anthophytes. Others group anthophytes with corystosperms alone, with glos-

sopterids and *Caytonia*, or with all three groups in various orders. When euglossopterids are the closest relatives of anthophytes, pinnately organized simple leaves and non-abaxial pollen sacs are synapomorphies of the two groups.

Other trees diverge more fundamentally in grouping *Caytonia* directly with angiosperms, based on reticulate venation and flat guard cells. In one (Fig. 12b), the resulting *Caytonia*-anthophyte clade is most closely related to corystosperms; in another (Fig. 12c), to glossopterids. Strictly speaking, this arrangement breaks up the anthophytes, but angiosperms plus *Caytonia* are still the closest relatives of the remaining groups; it might as well be said that these trees move *Caytonia* into the anthophytes. They require that anthophyte features lacking in *Caytonia* (simplified leaves, syndetocheilic stomata, flowers, granular exine structure) either arose independently in angiosperms and other anthophytes or were lost in *Caytonia*. In contrast, the shortest trees we found with angiosperms linked directly with glossopterids were 128 steps.

The 124-step trees again show the instability of relationships among platyspermic groups, but they agree in implying that the strongest affinities of anthophytes are with *Caytonia*, glossopterids, and/or corystosperms.

Since one of the main bases for linking anthophytes with *Caytonia* is the potential homology between the anatropous bitegmic ovules of angiosperms and the cupules of *Caytonia*, it should be noted that this homology implicitly requires that both structures are derived from circinately enrolled leaflets with ovules on their *adaxial* surface. This requirement is not based on the fact that angiosperm ovules are borne on the adaxial side of the carpel, but rather on the positions of the nucellus plus inner integument (presumably corresponding to the original unitegmic ovule), the funicle (the basal part of the leaflet), and the micropyle (its reflexed tip) relative to the rest of the carpel (Doyle, 1978, p. 384). We did not include adaxial vs. abaxial ovule position in the data matrix, because the relevant information is lacking or uncertain in many critical groups. As discussed in **Appendix III**, Harris (1940) presented strong, indirect evidence that cupules of *Caytonia* are in fact oriented adaxially, but this is questioned by Retallack (pers. comm.). One reason for doubt is that ovule position has been interpreted as abaxial in other platyspermic groups, such as *Callistophyton* and peltasperms (cf. Meyen, 1984). However, it is not clear that this is always the case: according to Rothwell (pers. comm.), ovule position is uncertain in *Callistophyton,* and Halle (1929) interpreted apparently platyspermic seed ferns from the Permian of China as having adaxial ovules.

Similar considerations apply to the cupules of glossopterids. These were clearly borne on the adaxial side of a blade-like structure, but there is disagreement on how they were oriented. Gould and Delevoryas (1977)

reconstruct a unicupulate form with the ovule-bearing surface of the cupule facing the subtending blade; if this is correct, ovule position would be an obstacle to a direct relationship between angiosperms and glossopterids. Retallack and Dilcher (1981) attempted to circumvent this problem by comparing angiosperms with the glossopterid genus *Denkania,* which apparently has orthotropous uniovulate cupules, and by interpreting angiosperms as originally orthotropous. However, this may have been unnecessary, since Pant and Nautiyal (1984) have recently reported that ovules in at least one glossopterid fructification (*Ottokaria*) were oriented adaxially. More conclusive evidence on cupule morphology and orientation in glossopterids and Mesozoic seed ferns could significantly modify the relative plausibility of hypotheses on anthophyte relationships.

C. ALTERNATIVE RELATIONSHIPS WITHIN THE ANTHOPHYTES

Other experiments were designed to evaluate alternative arrangements of groups within the anthophyte clade. Some such rearrangements have already been seen in trees where anthophytes are linked with groups other than Mesozoic seed ferns.

We found several trees with angiosperms the sister group of Bennettitales (rather than all other anthophytes) that are only two steps longer (125 steps) than the best trees. One of these is of the neo-englerian type, while the others associate anthophytes most closely with corystosperms rather than *Caytonia* (Fig. 13a), partly because reticulate venation is no longer a basic feature of anthophytes that favors closer links with *Caytonia* and glossopterids. Basically, this arrangement implies that simple megasporophylls with single orthotropous ovules (cupules) reverted to more complex megasporophylls with several pinnately arranged anatropous ovules in angiosperms, and microsporophylls reverted from whorled to spirally arranged. However, it saves steps by allowing only two origins of syndetocheilic stomata and one origin of scalariform secondary xylem, with no secondary losses.

Trees in which angiosperms are the sister group of Gnetales (Fig. 13b), as proposed by Crane (1985a), are nearly as parsimonious as those just discussed (126 steps). In all these trees, Bennettitales and *Pentoxylon* form a clade, as in Crane's scheme, based on orthotropous cupules and loss of reticulate venation. The extra steps are due either to independent reduction of the megasporophylls and whorling of the microsporophylls in Gnetales and Bennettitales plus *Pentoxylon,* or to secondary reversals in the same characters in angiosperms. As in Crane (1985a), the gnetalian-angiosperm link is supported only by characters that are not known in fossils and are therefore of indeterminate significance (in our data set, tunica, Mäule reaction, and siphonogamy).

Much less parsimonious results are obtained when angiosperms are

forced within Gnetales as the sister group of *Welwitschia* and *Gnetum* (Fig. 13c, 133 steps) or of *Gnetum* (Fig. 13d, 136 steps), as implied by suggestions that angiosperms are derived from Gnetales. Basically, these topologies require either that most of the advances linking the genera of Gnetales existed in the ancestors of angiosperms but were later lost, or that they originated twice. Evidently the potential synapomorphies between angiosperms and *Welwitschia* and *Gnetum* compensate for only a few of the resulting extra steps.

D. PATTERNS OF CHARACTER SUPPORT

Further insights into the robustness of inferred relationships among seed plant groups can be gained by comparing trees obtained by analyses of subsets of characters. Resulting observations on the nature of the character support for various schemes also suggest reasons why ideas on seed plant relationships have varied so much.

Not surprisingly, an analysis of vegetative characters alone (1–24) associated coniferopsids with *Archaeopteris*, corystosperms with *Medullosa*, Bennettitales with cycads, and angiosperms with *Caytonia* and glossopterids (Fig. 14a). Still, Gnetales are the closest living group to angiosperms, and we found a tree only one step longer in which the two groups are associated, with *Gnetum* basal in Gnetales, next to angiosperms. Both most parsimonious trees found when we analyzed macro-reproductive characters alone (25–42) move Gnetales into the coniferopsids and associate angiosperms with corystosperms and *Caytonia*. One tree links Bennettitales and *Pentoxylon* with corystosperms and angiosperms (Fig. 14b), while the other nests them in the coniferopsids, with Gnetales. In trees derived from micro-reproductive characters (43–62), Mesozoic seed ferns, glossopterids, and anthophytes form a clade; the coniferopsid groups are nested within seed plants but no longer form a clade (Fig. 14c). Anthophytes are a monophyletic group in some trees, but in others corystosperms are nested within them. In some, Bennettitales move into Gnetales, but *Welwitschia* and *Gnetum* are always linked.

On the whole, these experiments support the relationship of the anthophyte groups to one another and to Mesozoic seed ferns, although some character subsets do suggest alternative placements of some taxa. The alternative placement of coniferopsids with *Archaeopteris* is most supported by vegetative characters, and association of Gnetales with coniferopsids is most supported by macro-reproductive characters. As discussed in relation to the neo-englerian trees, it is relatively easy to accept the macro-reproductive similarities between Gnetales and coniferopsids as convergences, since many of them represent reduced states. Micro-reproductive characters give the results closest to those derived from the
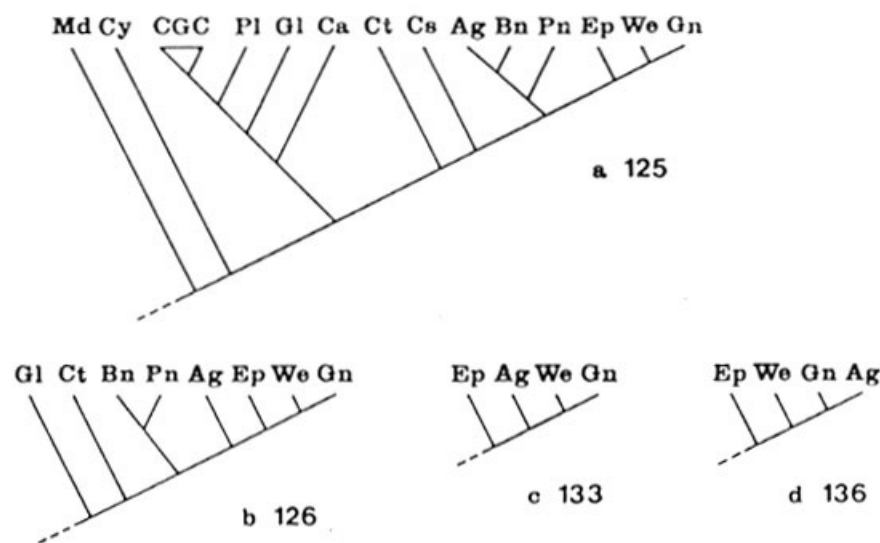
Fig. 13. Experiments with alternative relationships within the anthophytes, with numbers of steps indicated. (a) One of several most parsimonious trees obtained with angiosperms forced together with Bennettitales. (b) Most parsimonious tree obtained with angiosperms forced together with Gnetales. (c) Most parsimonious tree obtained with angiosperms forced into Gnetales, with *Welwitschia* and *Gnetum*. (d) Most parsimonious tree obtained with angiosperms forced into Gnetales, with *Gnetum*. CGC = conifers, ginkgos, and cordaites. In 13a and 13b, groups not indicated are arranged as in Figure 4; in 13c and 13d, they are arranged as in 13b.

whole data set, particularly in strongly supporting Mesozoic seed fern-anthophyte relationships and the link between *Welwitschia* and *Gnetum*. However, although micro-reproductive data support the hypothesis that coniferopsids are derived from seed fern-like ancestors, vegetative and macro-reproductive data are needed to show that coniferopsids are a monophyletic group.

Consistency indices for these trees indicate that the most homoplasy must be assumed in vegetative characters (C = 51), intermediate levels in macro-reproductive characters (C = 56), and the least in micro-reproductive characters (C = 65). The same trend is seen when consistency indices are calculated for these subsets of characters on the 123-step tree in Figure 4 (C = 43 for vegetative, C = 51 for macro-reproductive, C = 58 for micro-reproductive). These trends agree with conventional botanical intuition on the relative value of different sorts of characters (at least in this group). However, all sets of characters show some congruent patterns and thus provide significant information on relationships, and a priori elimination of characters could not be defended.
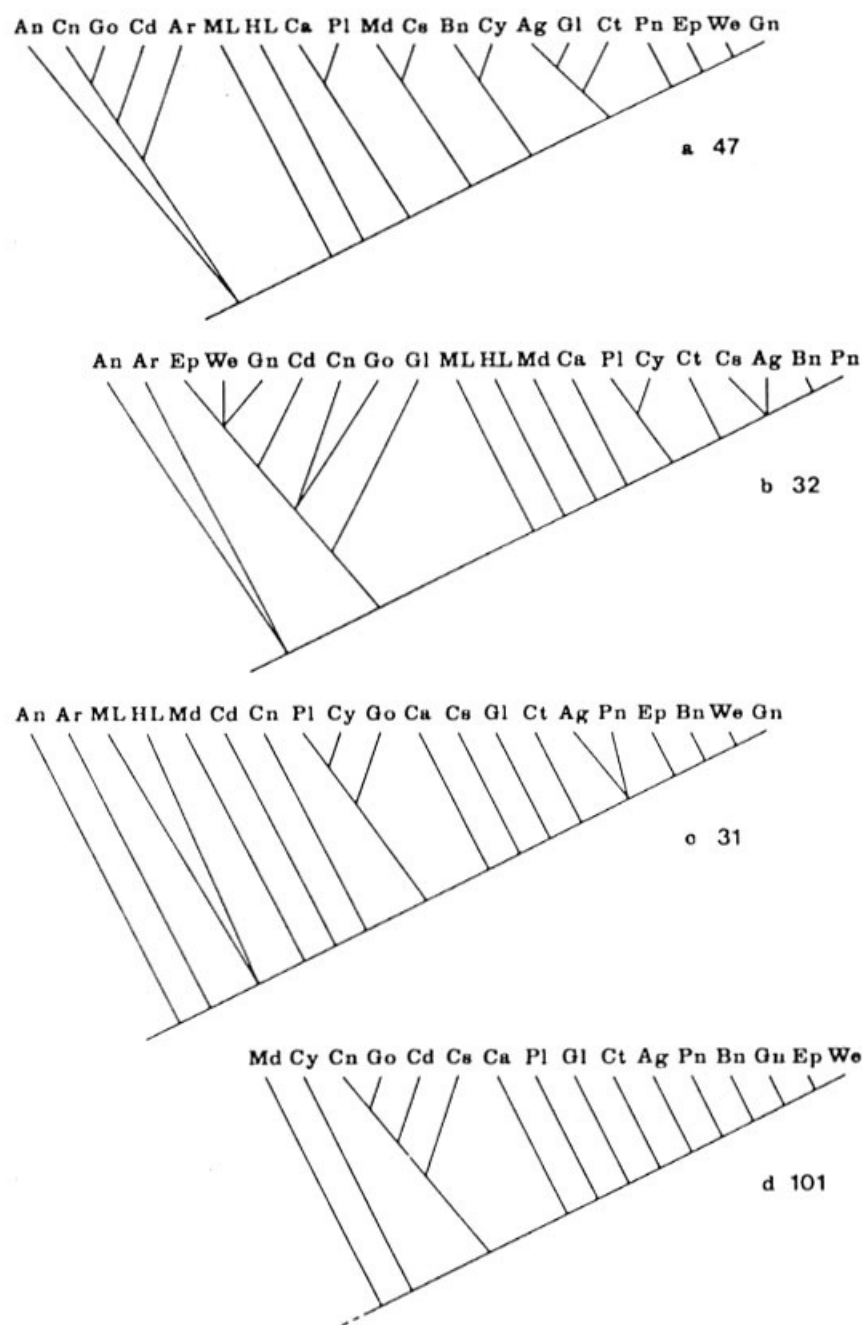
Removal of 12 anatomical, chemical, and embryological characters that are rarely or never preserved in Mesozoic groups (13, 16, 17, 18, 24, 55, 57–62) had little effect, showing that the inferred relationships between angiosperms and Gnetales are not simply an artifact of incomplete information on fossils. The tree obtained (Fig. 14d) differs from one of our most parsimonious trees only in making *Gnetum* rather than *Ephedra* the basal taxon in Gnetales, underlining the importance of embryological characters in uniting *Welwitschia* with *Gnetum*.

While these results confirm that different suites of characters may provide conflicting indications on seed plant relationships, there is reason to believe that several aspects of our preferred scheme may actually be stronger than implied. Thus there are several additional characters that we eliminated from the original data set because of uncertainty concerning definition, polarity, homologies of parts, or distribution in critical groups that may in hindsight support inferred relationships. Features of *Callistophyton*, cordaites, and ginkgos that might support the Rothwell hypothesis include secretory cavities and a similar sclerotesta-sarcotesta differentiation in the seed. Two more general seed plant characters that might have a similar effect are maceration-resistant cuticle, a feature of seed plants as opposed to ferns (Harris, 1932a), and a microgametophyte with a linear arrangement of prothallials and other cells. These were excluded because their state is unknown in progymnosperms, so that they do not definitely link coniferopsids with other seed plants rather than with *Archaeopteris*. However, because of its close functional integration with other aspects of reproduction, we suspect that at least the characteristic microgametophyte did not arise until during or after the origin of the seed.

Similarly, confidence in the idea that angiosperms, Bennettitales, and Gnetales are related is enhanced by the fact that they too show additional potential synapomorphies, plus several striking parallel trends. The latter cannot be used as synapomorphies (Rasmussen, 1983), but they may reflect shared genetic advances (Cantino, 1985). For example, as noted above, flower-like strobili, possibly bisexual, were presumably basic in anthophytes, and hence insect pollination may have been prevalent in the clade from its beginning. Ehrendorfer (1976) notes that Gnetales differ

←

Fig. 14. Results of analyses of subsets of characters, with numbers of steps indicated. (a) Most parsimonious tree based on vegetative characters alone (1–24). (b) One of two most parsimonious trees based on macro-reproductive characters alone (25–42). (c) One of several most parsimonious trees based on micro-reproductive characters alone (43–62). (d) Most parsimonious tree obtained after exclusion of 12 characters rarely or never preserved in Mesozoic groups (13, 16–18, 24, 55, 57–62); groups below Md arranged as in Figure 4.

from other gymnosperms and resemble angiosperms in having relatively small chromosomes, less repetitive DNA, and extensive polyploidy. In Gnetales there is also fusion of the second sperm nucleus with a nucleus of the megagametophyte (the ventral canal nucleus in *Ephedra,* another potential egg nucleus in *Gnetum:* Martens, 1971), which might be regarded as a precursor of double fertilization of the angiosperm type. Anthophytes also show strong tendencies for adaptation to hot and/or dry conditions. This is clearest for the angiosperms and Gnetales, which the pollen record shows were most abundant and diversified most vigorously in the Early Cretaceous of the African-South American tropical belt, associated with geological and paleobotanical evidence of aridity (Brenner, 1976; Doyle et al., 1977, 1982). However, it is also true for the Bennettitales, which had a predominantly low-latitude distribution and were one of the dominant groups in southern Eurasia during the Late Jurassic, a time of widespread aridity (Vakhrameev, 1970). An exception is *Pentoxylon:* its short shoots, pycnoxylic wood, naked unisexual flowers, and austral distribution suggest that it was specialized for temperate conditions (Drinnan & Chambers, 1985). Angiosperms and Gnetales also show parallel trends for acceleration of the life cycle and associated paedomorphic structural features (i.e., progenesis), and some tendency in this direction may also be suspected in Bennettitales and *Caytonia,* considering their small seed size relative to other gymnosperms. There is also preliminary evidence that Early Cretaceous angiosperms and Gnetales tended to occupy similar disturbed flood plain habitats (Doyle & Hickey, 1976; Doyle et al., 1982; Upchurch & Crane, 1985), supporting the idea that they were colonizing species, as proposed for early angiosperms by Stebbins (1974). The remarkable vegetative similarities between angiosperms and *Gnetum* are also easier to understand if they represent parallel responses to similar selection pressures acting on plants with a relatively recent common ancestor, rather than on members of very distantly related clades.

V. The Origin and Rise of Angiosperms

A. ALTERNATIVE SCENARIOS FOR THE ORIGIN OF ANGIOSPERMS

Further implications of our results for evolutionary events involved in the origin of angiosperms may be discussed with reference to Figure 15, which contrasts three almost equally parsimonious phylogenetic trees (cladograms with added information on time and possible ancestor-descendant relationships: Eldredge & Cracraft, 1980), with *Pentoxylon* omitted for clarity. We have shown Gnetales as extending to the Triassic, based on the presence of striate "ephedroid" pollen, but this is uncertain: putatively associated megafossils (the conifer-like genus *Dechellyia:* Ash, 1972) are less clearly gnetalian (although they do have opposite leaves),
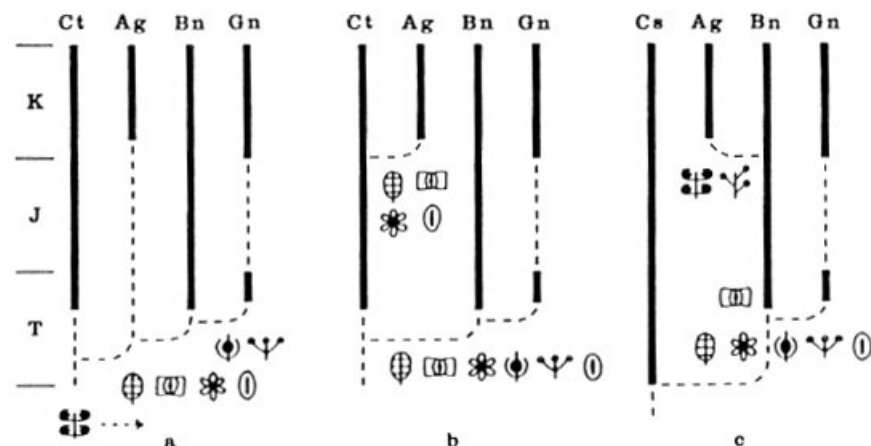
Fig. 15. Alternative scenarios for evolution of angiosperms and related groups, with *Pentoxylon* omitted for clarity. Solid lines indicate known stratigraphic ranges of groups; dotted lines, implied gaps in the fossil record. (a) Angiosperms as the sister group of other anthophytes, as in our most parsimonious trees; (b) angiosperms derived from some species of *Caytonia;* (c) angiosperms derived from some species of Bennettitales. T = Triassic, J = Jurassic, K = Cretaceous, Ct = *Caytonia,* Ag = angiosperms, Bn = Bennettitales, Gn = Gnetales, Cs = corystosperms. Characters indicated (reading left to right and down in 15a): solitary orthotropous cupulate ovule; whorled microsporophylls; once-pinnate leaf; syndetocheilic stomata; sporophylls aggregated into flowers; granular monosulcate pollen; pinnate megasporophyll with anatropous cupulate ovules.

and there is a gap in the record of ephedroid pollen through most of the Jurassic.

Figure 15a corresponds to all of our most parsimonious (123-step) cladograms, in which angiosperms are the sister group of all other anthophytes (Figs. 4, 5). As already noted, this scheme sees syndetocheilic stomata, non-saccate, granular pollen, aggregation of sporophylls into flowers, and probably simplified leaves as features of the common ancestor of anthophytes, and reduced megasporophylls, whorled microsporophylls, and a micropylar tube as further advances of Bennettitales and Gnetales. A problem with this arrangement is that it entails a gap in the record of the angiosperm line from at least the Late Triassic to the Early Cretaceous. This could be taken as support for the idea that angiosperms existed well before the Cretaceous but were geographically or ecologically restricted (e.g., to the tropical uplands: Axelrod, 1952, 1970). The related idea that angiosperms underwent much of their radiation before the Cretaceous is contradicted by fossil evidence for rapid diversification of angiosperms during the Cretaceous, but existence of primitive angiosperms with monosulcate pollen before the Cretaceous cannot be ruled out (Doyle, 1969, 1978; Muller, 1970). Reports of Late Triassic monosulcate pollen with

tectal perforations and columellae (Cornet, 1977) and Jurassic dicot-like leaves (*Phyllites,* etc.: Crane, 1985a) might be taken as support for the latter hypothesis.

If fully developed angiosperms existed in the Triassic, it is hard to understand why they did not radiate until the Cretaceous. An alternative hypothesis is that many advances (autapomorphies) of angiosperms did not evolve in the angiosperm line until the Cretaceous. In fact, our scheme predicts that early members of the line might be essentially indistinguishable from Bennettitales in leaf morphology and anatomy, stem anatomy (except for multi- or trilacunar nodes), and pollen morphology—i.e., in most respects except for multicupulate megasporophylls and spiral microsporophylls (cf. Arber & Parkin, 1907). This highlights the need for a search for reproductive structures associated with the many "bennettitalian" leaf genera that are known only as isolated organs. If the record of other adaptive radiations is any guide, it is quite likely that a great variety of experimental anthophyte lines existed in the Triassic and Jurassic, of which the known groups are only the most successful.

In Figure 15b, angiosperms are derived from some species of *Caytonia,* making *Caytonia* a paraphyletic group. Since *Caytonia* is more primitive than angiosperms in all characters considered, this tree agrees in both topology and number of steps with our 124-step cladograms with angiosperms the sister group of *Caytonia* (Fig. 12b, 12c). Here flat guard cells are homologous in the two groups rather than convergent, but syndetocheilic stomata, simplified leaves, granular exines, and flowers originated separately in angiosperms and the bennettitalian-gnetalian line. Because of the arrangement of other groups in the corresponding cladograms, it is most parsimonious to assume that saccate pollen originated separately in *Caytonia* and corystosperms; however, we suspect that this would change with better information on platyspermic groups. In tree 15b, insect pollination and the ability to colonize unstable and/or arid habitats probably arose independently in angiosperms and Bennettitales plus Gnetales, since there is little evidence for these features in *Caytonia* or other Mesozoic seed ferns. However, the small seed size and reduction of the megaspore wall in *Caytonia* could be taken as evidence that the inferred trend for progenetic acceleration of the life cycle had begun in the common ancestor of angiosperms, *Caytonia,* and other anthophytes. This tree has the advantage of eliminating the stratigraphic gap in Figure 15a: angiosperms could have originated at any time up to the Cretaceous. A major weakness of this scheme is that most of the characters that potentially support the basal anthophyte-*Caytonia* node are unknown in key fossil groups. This is also somewhat true of anthophyte relationships, since several such characters (tunica, lignin chemistry, siphonogamy) are undocumented in Bennettitales and *Pentoxylon,* but not only these but also

scalariform pitting and endarch primary xylem are unknown in *Caytonia.* Information on any of these characters in *Caytonia* could affect the plausibility of this scheme.

In the third tree (Fig. 15c), angiosperms evolved from some member of the Bennettitales, making Bennettitales a paraphyletic group. This corresponds in topology to cladograms in which angiosperms and Bennettitales are sister groups (Fig. 13a), which were two steps longer than the shortest trees, but it involves a few extra steps corresponding to loss of what have been assumed to be bennettitalian autapomorphies. Basically, this tree requires changes in angiosperms from simple megasporophylls with single orthotropous cupules to leaf-like carpels with several anatropous bitegmic ovules, from whorled to spirally arranged microsporophylls, and from unilacunar to multilacunar nodes, and loss of the micropylar tube, secretory canals, and interseminal scales.

Despite these extra steps, this hypothesis has several intriguing features that make it worth future consideration. Like Figure 15b, it eliminates the stratigraphic gap entailed by Figure 15a. Furthermore, reinterpretations of basic conditions and arrangements of groups within angiosperms that decrease the number of steps involved are not inconceivable. For example, nodal anatomy is fairly diverse within magnoliids, and although we favor arguments that multi- or trilacunar nodes are ancestral, this is controversial (Bailey, 1956; Benzing, 1967; Takhtajan, 1969). Likewise, orthotropous ovules are typical of one monosulcate magnoliid order, Piperales, including the Chloranthaceae, which have pollen and leaves similar to some of the oldest Cretaceous angiosperm fossils (Muller, 1981; Upchurch, 1984; Walker, 1976), and which some have suggested are more primitive than generally assumed (Burger, 1977; Meeuse, 1972a, 1972b). Loss of the micropylar tube might be expected on functional grounds once the ovules were enclosed in the carpel, and some angiosperms have a protruding inner integument that might be interpreted as a vestige of the tube (Maheshwari, 1950). It is also not established that all Bennettitales had secretory canals. Since the Bennettitales were a diverse group, it is possible that derived similarities will be found between angiosperms and particular Bennettitales, which would strengthen the idea that Bennettitales are paraphyletic. For example, if it can be established that unisexual flowers are basic in Bennettitales (as assumed by Crane, 1985a), bisexual flowers (as in *Williamsoniella* and *Cycadeoidea*) could be a synapomorphy of some Bennettitales and angiosperms.

Perhaps the most important change required in derivation of angiosperms from a bennettitalian ancestor, derivation of carpels from stalked ovules, is much harder to imagine. However, S. V. Meyen (pers. comm., 1984) suggested a highly speculative but intriguing mechanism that would produce the same result, parallel to the hypothesis of Iltis (1983) that the

ear of maize originated not by elaboration of the two-ranked pistillate inflorescence of teosinte, but rather from the more complex staminate inflorescence by a regulatory shift to production of pistillate flowers (gamoheterotopy). Meyen points out that some Bennettitales had relatively leaf-like microsporophylls with microsynangia borne in two rows on the adaxial surface; a mutation leading to extension of the developmental program for such structures to the ovuliferous portion of a bisexual floral axis could result in flat megasporophylls with cupules substituted for microsynangia. These structures would be closer to the hypothetical primitive carpel than any known gymnosperm megasporophyll. Such a substitution might automatically result in elimination of another obstacle to derivation of angiosperms from the Bennettitales, interseminal scales, which are generally assumed to be derived from megasporophyll primordia. Other possibilities are that carpels arose by modification of interseminal scales and their association with ovules, or by reactivation of suppressed developmental pathways for production of the more complex megasporophylls of the ancestors of anthophytes.

Since many of the features that constitute obstacles to a bennettitalian origin of angiosperms are shared by Gnetales, such reinterpretations would also increase the plausibility of a direct relationship between angiosperms and Gnetales (Fig. 13b), as proposed by Crane (1985a), especially if any additional "gnetalian" features were also reinterpreted as basic within angiosperms. Again, candidates for such characters exist in the Chloranthaceae (opposite leaves; two-trace, swollen nodes; inflorescences composed of small, apetalous flowers with uniovulate carpels). However, Gnetales still have so many additional advances over angiosperms (e.g., pitting, lack of a cupule homolog, striate pollen) that a sister group relationship would be far more likely than derivation of angiosperms from some member of Gnetales.

Because of the autapomorphies of Bennettitales, it is most parsimonious to assume that the Gnetales (with or without *Pentoxylon*) were derived from a common ancestor with the Bennettitales, rather than being highly modified bennettitalian derivatives, as suggested by Takhtajan (1969) and Ehrendorfer (1976). However, the latter hypothesis is hardly ruled out; the presumed autapomorphies of Bennettitales are probably less serious obstacles to a bennettitalian origin of Gnetales than of angiosperms. One, unilacunar nodes, may actually have been an intermediate condition between multilacunar and two-trace; secretory canals may not have been present in all Bennettitales; and interseminal scales might be expected to disappear during the inferred floral reduction. This suggests the further possibility that angiosperms and Gnetales were both derived from a bennettitalian line that began a trend for leaf simplification and floral reduc-

tion and aggregation (perhaps as late as the Jurassic), which was continued in Gnetales but reversed in angiosperms.

B. CAUSAL FACTORS IN THE ORIGIN OF ANGIOSPERMS

These schemes help put in clearer perspective possible causal factors in the origin of angiosperms. In order to identify such factors, traits that actually evolved in the angiosperm line after its separation from its sister group must be distinguished from those already present in the common ancestor of angiosperms and related groups. Traits of the latter sort are not directly relevant to the origin of angiosperms, but instead require explanation at another level. Traits that arose in the angiosperm line need to be explained whether they are now universal in angiosperms or have since been transformed within the group, and whether they evolved only in angiosperms or independently in some other group(s). Which traits are believed to belong to these various categories directly depends on presumed relationships within angiosperms and between angiosperms and other groups, and it is precisely this sort of information that cladistic analysis provides. In order to relate this information to reasons for the origin of angiosperm traits, one can and should consider evidence concerning paleoenvironments occupied by early angiosperms and their relatives, development, and functional morphology (ideally relating the presence of traits to fitness). Clearly this "scenario" level of analysis is fraught with difficulties, but as Eldredge (1979) has pointed out, it is the most fun, and it can be a useful exercise if it is based squarely on cladograms and generates testable ideas.

In specific terms, the scheme in which angiosperms are directly linked with *Caytonia* (Fig. 15b) implies that the origin of flowers, insect pollination, adaptation to unstable and/or arid habitats, and acceleration of the life cycle all need to be explained in order to understand the origin of angiosperms, since they all arose independently in angiosperms and in other groups. This corresponds most closely to the assumptions implicit in the discussions of Stebbins (1974), Doyle and Hickey (1976), and Doyle (1978, 1984). However, under schemes in which angiosperms are the sister group of Bennettitales plus Gnetales (Fig. 15a), which we now find preferable, these same features were presumably established at an earlier stage in the evolution of the anthophyte clade. The same is true if angiosperms were derived from Bennettitales (Fig. 15c). Under all three schemes, broad leaves with a hierarchy of reticulate venation, vessels, one-veined microsporophylls, and reduced gametophytes evolved independently in angiosperms and Gnetales, while the closed carpel, stigmatic pollen germination, and double fertilization with associated endosperm formation arose only in angiosperms.

As emphasized by Takhtajan (1969, 1976), many conspicuous differences between angiosperms and gymnosperms can be interpreted in terms of paedomorphosis (the phylogenetic shifting of juvenile features to later stages of ontogeny): the simple leaves and stamens suggest leaf primordia before initiation of leaflets; scalariform pitting in the secondary xylem could be due to extension of the metaxylem pitting pattern; flowers resemble shoots before elongation of the internodes; closed carpels suggest unopened conduplicate leaves; the ovules are in a primordial state at the time of fertilization; and the three-nucleate microgametophyte, the partly free-nuclear condition of the megagametophyte, and the lack of archegonia could be effects of truncation of development. As noted above, Doyle (1978) pointed out that the small size and early functioning of most of the structures concerned suggest that they originated by progenesis (paedomorphosis due to precocious maturation, as distinguished from neoteny, paedomorphosis due to retardation of development). Since Gould (1977) associated progenesis with selection for rapid reproduction, this would fit fossil evidence that early angiosperms were colonizing species (Doyle & Hickey, 1976; Stebbins, 1974). Under the schemes in Figure 15a and 15c, the situation is more complex: some paedomorphic traits (gametophyte reduction, small simplified stamens, carpel closure) arose in the angiosperm line, but others are basic for anthophytes as a whole (scalariform pitting, aggregation of sporophylls, small seeds with a reduced megaspore wall). This suggests that factors favoring progenesis were operating on the anthophytes since their origin, but they were continued and intensified independently in angiosperms and Gnetales. This is consistent with the fact that all three major anthophyte groups show evidence of adaptation to arid and/or disturbed environments (e.g., stream margin facies), but this tendency is most striking in early angiosperms and Gnetales (Brenner, 1976; Crane, in press; Doyle & Hickey, 1976; Doyle et al., 1977, 1982; Upchurch & Crane, 1985; Vakhrameev, 1970).

The vessels and leaf architecture of angiosperms may also be explained in terms of original adaptation to seasonally arid conditions (cf. Stebbins, 1974), and it may be significant that these are among those features that evolved independently in Gnetales. Thus the geographic distribution of Early Cretaceous angiosperms and Gnetales supports the idea that vessels originated as an adaptation to aridity, as suggested for Gnetales (but not angiosperms) by Carlquist (1975). The inferred relationships of the genera of the Gnetales suggest that the first Gnetales resembled the xerophytes *Ephedra* and *Welwitschia* in having linear leaves, while *Gnetum*, tropical rain forest trees or lianas with dicot-like leaves, is more advanced. Together with the paleogeographic evidence, this suggests that the dicot-like leaves of *Gnetum* originated by expansion of linear leaves during or after secondary invasion of wet habitats. Whether the similar leaves of dicots

arose from reduced xeromorphic precursors by a similar series of events, as speculated by Doyle and Hickey (1976), cannot be determined without better information on the ancestral leaf type in anthophytes or in earlier members of the angiosperm line, but this scenario would be consistent with the inferred parallels between the ecological histories of angiosperms and Gnetales. From an ecophysiological point of view, vessels may have been a prerequisite for evolution of large, undissected leaves in the tropics, since such leaves should tend to overheat even in wet tropical conditions unless vessels are present to allow rapid transpiration (Doyle et al., 1982). In keeping with this expectation, the few known tropical Early Cretaceous megafossil floras are noteworthy for being dominated by highly xeromorphic "brachyphyll" conifers (Cheirolepidiaceae, Araucariaceae), small-leafed Bennettitales, and the xeromorphic fern *Weichselia*, even when associated with coals indicating wet conditions (Berry, 1939; Doyle et al., 1982; Smiley, 1970).

C. FACTORS IN THE RISE OF ANGIOSPERMS

Our results may also shed light on reasons for the spectacular success of angiosperms, which need not be related to factors involved in their origin. First, it is important to recognize that "success" may be measured by at least three criteria: (1) persistence or longevity of a clade; (2) ecological dominance, reflecting the abundance of individual organisms and/or the range of environments occupied; and (3) diversity, or the number of species. These criteria are often not clearly separated, and explanations (such as "key adaptations") that might account for one element of success are extended, usually implicitly, to the other elements. Although it is conceivable that a single factor might simultaneously affect all three elements positively, this certainly need not be the case. Some clades have existed for a very long time but have apparently never been dominant or diverse (e.g., horseshoe crabs, *Selaginella*), while others are spectacularly speciose but not dominant (e.g., orchids), and others have been ecologically dominant but not unusually diverse or long-lived (e.g., glossopterids in the Permian of Gondwana, cheirolepidiaceous conifers in the Jurassic and Cretaceous, humans). The last phenomenon demonstrates that an advance in design (simple, deciduous leaves; xeromorphy; large brains) may lead to an increase in the number or biomass of organisms with the trait but not necessarily to an increase in the number of species; in the case of humans, it may even have had the reverse effect. There is no question that angiosperms are highly successful in terms of both ecological dominance and species diversity, but their success as measured by group longevity depends on their exact relationships with *Caytonia*, Bennettitales, and Gnetales.

Recently the relative diversity of clades has attracted special attention,

and it is now recognized that at one level this is a function of differences in speciation and extinction rates (Gould & Eldredge, 1977; Stanley, 1979; Vrba, 1983). It has also become evident that the relationship between traits (whether of individual organisms or emergent at the level of populations or species) and rates of speciation and extinction is complex. A ubiquitous trait in a diverse clade cannot be assumed to be the cause of its diversity, even if its adaptive value is undisputed. As Vrba (1983) pointed out, some traits may have incidental effects on speciation rate, and other features might rise in frequency simply by association with such traits. Similarly, characteristics that affect the size of geographic ranges may incidentally affect both speciation and extinction rates (Jablonski, 1986; Jablonski et al., 1985). Drawing an analogy between the ecological concepts of r- and K-strategies and macroevolutionary phenomena, Gould and Eldredge (1977) argued that whereas some "survivor" clades may be diverse and long-lived (i.e., resistant to extinction) by virtue of superior competitive abilities, "increaser" clades may be successful simply as a result of higher speciation rates, which for example may allow them to exploit new opportunities made available by geological disturbances.

These ideas may be applied to the question of success of the angiosperms by considering possible relationships between particular angiosperm apomorphies and speciation and extinction rates. In part, the ecological amplitude and dominance of angiosperms could be a function of the combination of vessels and intercalary meristems, allowing leaf expansion (Stebbins, 1974, 1981), which we have argued may have allowed angiosperms to exploit tropical habitats far more effectively than earlier groups. However, this only reaffirms the need for an additional explanation for both the dominance and the diversity of angiosperms, since *Gnetum* has the same features but consists of only a few stereotyped species that play a minor role in the present vegetation (cf. Doyle, 1978, 1984). Furthermore, there is no obvious link between presence of vessels and/or broad leaves and rate of speciation (though intercalary meristems might permit production of a greater diversity of designs in the long term, as stressed by Stebbins, 1974, 1981).

Several authors have suggested that insect pollination might have the effects on speciation and extinction rates required to explain the diversity of angiosperms (Burger, 1981b; Doyle, 1984; Doyle et al., 1982; Janzen, 1970; Regal, 1977; Stanley, 1979; but see Stebbins, 1981). Insect pollination might indirectly favor not only higher speciation rates, by making possible pollinator-mediated isolating mechanisms, but also lower extinction rates, by allowing angiosperm species to maintain more dispersed distributions of individuals than wind-pollinated gymnosperms, which might improve their ability to escape herbivores and pathogens. However, if Mesozoic Bennettitales and Gnetales were also insect-pollinated, the

same factors should have been operating on them as well, and in fact Doyle (1984) suggested that this might explain their abundance and diversity in the Cretaceous tropics. This leaves open the question of why angiosperms diversified even more and eventually replaced other anthophytes. Furthermore, under either our favored scenario (Fig. 15a) or derivation of angiosperms from Bennettitales (Fig. 15c), insect pollination probably existed in the angiosperm line since the Triassic, leaving open the question of why angiosperms did not radiate until the Cretaceous.

These considerations underline the need to identify more specific angiosperm apomorphies that might have resulted in a sharp increase in diversification over other anthophytes and early members of the angiosperm line. We suggest that closure of the carpel may have had such an effect. Carpel closure might result in increased speciation rates by allowing experimentation with new means of dispersal (independent of seed modifications) and hence more frequent establishment of geographically isolated populations. Regal (1977) and Burger (1981b) have suggested that greater dispersal potential would act in concert with insect pollination in allowing more dispersed distributions of individuals and hence lead to a decrease in extinction rate. Carpel closure also entails germination of pollen on a stigma, which might increase the probability that mutations would result in blocks to germination or growth of pollen from partly differentiated populations, which might in turn set the stage for character displacement operating on parapatric populations (Burger, 1981b). This should not be confused with the hypothesis that stigmatic germination favors pollen competition, which might result in more vigorous, competitively superior sporophytes (Mulcahy, 1979); this may be an important phenomenon, but it is not clear that it would result in an increased speciation rate.

Since every speciation event can be viewed as an evolutionary experiment, it is possible that increased speciation rate itself may have been indirectly responsible for the dominance of angiosperms (Doyle, 1984; Stanley, 1979). There is no evidence of catastrophic events that might have opened up major adaptive zones for angiosperms (Knoll, 1984). However, the ability to generate new species at a high rate might have led in the long term to occupation of more and more of the adaptive landscape by angiosperms and their piecemeal replacement of other groups, whether by occupation of niches vacated by "background" extinction due to physical and biotic factors unrelated to the occurrence of angiosperms, or by direct competition between particular gymnosperms and particular new angiosperm species. In either case, this contrasts with the view of Knoll (1984) that the replacement of older groups by angiosperms was due to their basically superior competitive abilities: in our view, their success is due not to any competitively advantageous feature(s) common

to all angiosperms, but rather to the fact that they consist of such a wide array of adaptive types, as a consequence of high speciation rates. The origin of a powerful and highly flexible array of chemical defenses against herbivores, another factor discussed as a key to the success of angiosperms (Tiffney, 1981), may be viewed in the same way.

We note that these proposed mechanisms for the rise of angiosperms exemplify a general phenomenon wherein a trait selected at the level of organisms, once evolved, has incidental effects on rates of speciation or extinction, possibly through its influence on population structure (cf. Vrba, 1983; Vrba & Eldredge, 1984).

VI. Conclusion

Although the scenarios just presented are necessarily speculative and leave many questions unanswered, we believe that the cladistic analyses on which they rest provide a much clearer picture of the relative merits of competing hypotheses on seed plant phylogeny and focus attention on several that require special consideration. Our analyses make a great number of detailed predictions on character state changes and the morphology of fossil groups that are subject to testing by future work. On the neontological front, a fruitful approach to angiosperm relationships in particular may be study of appropriate DNA sequences, which should show much closer relationships between Gnetales and angiosperms (which probably diverged as recently as the Triassic) than between any of the other major extant seed plant groups (which diverged at least as early as the Carboniferous). On the paleobotanical front, information on cryptic characters in Bennettitales (meristem type, lignin chemistry, embryology) and on anatomy and cupule orientation in *Caytonia* and other platyspermic groups could be especially critical. We also suggest that more attention be paid to elucidation of the anatomy and reproductive structures of Triassic and Jurassic fossils that have been assigned to Bennettitales, which may include previously unrecognized anthophyte taxa. Finally, future cladistic analyses of angiosperm subgroups in the context of anthophyte relationships may help resolve outstanding problems of angiosperm phylogeny and lead to a better understanding of early angiosperm evolution.

VII. Acknowledgments

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Appendix I: Taxa Used

Here we list terminal taxa used in the analysis, with abbreviations used in the figures, known stratigraphic ranges, reasons for inclusion or exclusion of groups, and possible autapomorphies that support their monophyly.

Apparent synapomorphies of all lignophytes are listed in the text. Of these, secondary growth is not unique to lignophytes, but other occurrences appear to be independently derived within their respective groups. Lycopsid examples are clearly restricted to advanced groups and very different in detail (Lepidodendrales had only secondary xylem: *Isoëtes* has an anomalous mixture of xylem and phloem). Secondary growth also occurs in some sphenopsids and ferns, but it is probably not basic in either group, since it is lacking in their presumably most primitive members (Middle Devonian Cladoxylales-Hyeniales), and some cases differ in detail from lignophytes. Thus *Calamites* is supposed to have secondary xylem only, although *Sphenophyllum* has secondary phloem as well. The one example in living ferns is *Botrychium*, but Bierhorst (1971) suggests that this may be a progymnosperm derivative rather than a fern; in any case, because of the limited number of tracheids in radial files, there is doubt as to whether they are truly secondary. Secondary xylem, including rays (Taylor, 1981), is also reported in some zygopterid ferns (*Rhacophyton, Zygopteris*), but the amount of secondary tissue is limited.

An: *Aneurophyton* s. lat., including *Triloboxylon* and *Eospermatopteris* (Middle–Late Devonian). Chosen as representative of "Aneurophytales," which are probably paraphyletic; e.g., *Chaleuria* (with heterospory: Andrews et al., 1974) or *Proteokalon* (with tendencies toward distichous branching) may be closer to *Archaeopteris* and/or seed plants, while the oldest genus, *Protopteridium*, which is primitive in having scalariform pitting and an irregularly lobed stele, may be the sister group of all other lignophytes. No definite autapomorphies; some or all aneurophytes have complex secondary phloem, but this may be basic in lignophytes (Wight & Beck, 1984).

Ar: *Archaeopteris* s. lat., including late Middle Devonian *Svalbardia* (Middle Devonian–Early Carboniferous). *Svalbardia* differs from *Archaeopteris* s. str. in having helical rather than distichous branching, but it is uncertain whether this is a consistent difference, and the

two genera are otherwise similar (Beck, 1976). A possible autapomorphy is the presence of *Callixylon*-type pitting, but this is not established in *Svalbardia*.

Ml: a composite of Early Carboniferous protostelic "lyginopterids" with multiovulate cupules. Scored the same as *Pitus* in Doyle and Donoghue (1986), which was based on Long's (1979) proposed association of *Pitus* stems, *Lyginorachis* petioles, *Tristichia ovensi* fertile branches, *Stamnostoma* seeds and cupules, and *Telangium* pollen organs. This does not include Calamopityaceae, which may be associated with platyspermic, non-cupulate *Lyrasperma* seeds (Meyen, 1984; Retallack, 1985). No known autapomorphies, and almost surely paraphyletic, but retained in the analysis for reasons discussed in the text.

Hl: "higher lyginopterids," including *Heterangium* and *Lyginopteris* (Early–Late Carboniferous). *Heterangium* and *Lyginopteris* are generally considered closely related; Scott (1923) cited species of the two genera as illustrating a gradational series in origin of the eustele from a protostele by vitalization. A possible autapomorphy is the presence of radially elongated, ribbon-like hypodermal sclerenchyma strands, as opposed to the less elongated strands of other groups. The presence of a vitalized protostele and terminal microsporangia in *Heterangium* implies that the eustele and abaxial microsporangia of *Lyginopteris* arose within the group. Association of *Heterangium* with leaves and microsynangia on planated frond segments (*Telangium*) is firmly established (Jennings, 1976). This group may differ from the previous one in having uniovulate cupules (well known in *Lyginopteris*), based on Stewart's (1983) association of *Heterangium* with *Sphaerostoma* and *Conostoma* seeds. However, this needs confirmation, since although *Sphaerostoma* has been found in cupules, *Conostoma* is known only in isolation, and T. N. Taylor (pers. comm.) suspects that it may have been borne in multiovulate cupules, based in part on similarities in anatomy of *Conostoma* and seeds of the Late Carboniferous multiovulate cupule *Gnetopsis* (Taylor & Millay, 1981). In any case, uniovulate cupules would not be a definite autapomorphy, since this condition may have existed in the ancestor of all higher seed plants; this would certainly be true under the hypothesis that the lyginopterid cupule was transformed into the free integument of medullosans and other groups (Meyen, 1984; Walton, 1953), but it might be true even under other hypotheses on the fate of the cupule.

Md: *Medullosa* (Late Carboniferous–Permian). As explained in the text, we excluded probably related protostelic forms: *Quaestora* (Mapes & Rothwell, 1980) because only stems are known; and *Sutcliffia*, which has been associated with reticulate-veined leaves (*Linopteris*) and less securely with advanced pollen organs (*Potoniea*) but primitive trilete prepollen (Stidd, 1981), because of uncertain association and lack of seed characters. It is possible that even *Medullosa* in the narrow sense is paraphyletic, since definite autapomorphies are hard to identify. Internal secondary xylem, complex microsynangia, and large prepollen (*Monoletes*) have been traditionally considered terminal specializations. However, trends in Permian medullosan stems for loss of internal secondary xylem suggest that the medullosan stele may have given rise to at least some normal eusteles, and internal secondary xylem also occurs in corystosperms and *Pentoxylon*. Although such complex microsynangia as *Dolerotheca* appear to be a unique advance, the basic condition for the whole group, as represented by *Codonotheca*, is more generalized. Similarly, *Monoletes* is not always so large, and it has no other features that would rule out the possibility that it gave rise to other bilateral pollen types.

Ca: *Callistophyton* (Late Carboniferous). No definite autapomorphies.

Gl: Glossopteridales (Late Carboniferous–Early Triassic). Crane (1985a) lists several potential autapomorphies, but these are uncertain. Thus the *Glossopteris* leaf might be a prototype for the angiosperm type. Likewise, although mega- and microsporophylls adnate to the adaxial side of a leaf seem unique, Stebbins (1974) and Retallack and Dilcher (1981)

have suggested that the whole ovulate structure could have been transformed into an angiosperm carpel. Striate bisaccate pollen also occurs in Permo-Triassic conifers and peltasperms (Meyen, 1984).

Pl: *Peltaspermum* (*Lepidopteris, Antevsia*) (Permian–Triassic). Included as the best-reconstructed representative of Peltaspermaceae (Harris, 1932a; Townrow, 1960), which may be paraphyletic if defined as broadly as by Meyen (1984). Future studies might add *Tatarina* (with simple leaves) or other forms with striate pollen to the analysis as separate taxa, in order to test possible relationships with higher groups. Rachial blisters (resin cavities?) are a possible autapomorphy.

Cs: Corystospermaceae (*Dicroidium, Rhexoxylon, Umkomasia, Pteruchus*) (Triassic). Archangelsky (1968) adduces strong circumstantial evidence for association of *Rhexoxylon* stems with *Dicroidium* and hence the fertile structures. No definite autapomorphies.

Ct: *Caytonia* (*Sagenopteris, Caytonanthus*) (Late Triassic–Late Cretaceous). No definite autapomorphies; the palmately compound leaves could represent a stage in evolution of the simple condition.

Cy: Cycadales, including Nilssoniales (Late Triassic?–Recent). We have not included Late Carboniferous and Permian forms with simple, pinnately veined *Taeniopteris* leaves (*Spermopteris, Archaeocycas, Phasmatocycas*), considered early cycads by Mamay (1976), since they are reported to have platyspermic seeds, which Crane (1985a) argues excludes them from cycads and associates them instead with *Callistophyton* and peltasperms. However, the report that these forms were platyspermic needs confirmation, since it was based on compressed material, and even if it is correct it may not be an obstacle to relationship with cycads (see discussion in text). Given these uncertainties, it seems safer to consider only Mesozoic and modern members, and equally informative, since most of the same conclusions on basic conditions within cycads would be reached with or without consideration of the Paleozoic forms (see discussion of the leaf character).

Crane (1985a) lists simple ovulate cones as a cycad autapomorphy, but this requires interpreting the zones of megasporophylls alternating with vegetative leaves in *Cycas* as cones, which stretches the usual definition of cones as determinate structures. In this respect, *Cycas* may be no more advanced than Paleozoic seed ferns. Furthermore, according to Florin (1949), ginkgos too have simple ovulate cones, and this may have been the basic condition in coniferopsids as a whole, if aggregation of sporophylls on the secondary shoots of conifers and cordaites occurred before the aggregation of these shoots into compound strobili. Better autapomorphies may be sympodial formation of pollen cones and resulting "cone domes"; girdling leaf traces (potentially a modification of the medullosan situation); cycasin, a methylazoxymethanol glycoside (Crane, 1985a); and the unique pattern of simplification of the sporophylls (see characters 25–30).

Bn: Bennettitales (Late Triassic–Late Cretaceous). A preliminary cladistic analysis of 11 taxa is presented by Crane (1985a). In future analyses, it would be desirable to treat morphologically divergent groups as terminal taxa (e.g., the Late Triassic naked ovulate flower *Vardekloeftia*, which Crane interprets as the basal taxon, or the bisexual Jurassic genus *Williamsoniella*), in order to evaluate the possibility that Bennettitales are paraphyletic (see text for discussion). However, too few forms are well reconstructed at present.

The clearest autapomorphy is probably the presence of interseminal scales on the ovuliferous receptacle, believed to represent sterilized ovules (Crane, 1985a; Harris, 1932b). Of other autapomorphies cited by Crane (1985a), the characteristic pattern of cutinization of guard cells, particularly presence of cutinized lamellar guard cell thickenings (Harris, 1932a), has parallels in angiosperms (G. R. Upchurch, pers. comm.). Ovulate heads with numerous ovules could be primitive rather than advanced relative to the smaller ovule number in

Pentoxylon or the uniovulate condition in Gnetales, while bivalved microsynangia could have been reduced to the conditions in other anthophytes. Bennettitales differ from other groups in having stomata oriented perpendicular to the venation (the syndetocheilic stomata of *Welwitschia* are in the normal parallel arrangement: Florin, 1931; Martens, 1971), but the random condition in angiosperms, *Pentoxylon,* or *Gnetum* could have been derived from this.

Pn: *Pentoxylon* (Jurassic–Early Cretaceous). Based on more critical palynological studies, the original locality for *Pentoxylon,* the Rajmahal Hills flora, is probably Early Cretaceous rather than Jurassic (Varma & Ramanujam, 1984), and it is abundant in the Lower Cretaceous of Australia (Drinnan & Chambers, 1985). The three-dimensional microsporophylls may be autapomorphic, but this condition could have existed in the ancestry of Gnetales.

Cd: Euramerican cordaites, including *Cordaites, Cordaianthus,* and *Mesoxylon* (Late Carboniferous–Permian). We exclude Angaran forms such as *Rufloria* and *Vojnovskya* (Meyen, 1984), which lack the characteristic combination of compound male and female strobili and might better be treated as separate taxa. The clearest autapomorphy is probably the 4-ranked arrangement of fertile short shoots on a dorsiventral axis (Crane, 1985a); Crane also cites "*Cordaites* foliage," but this could be a precursor to other coniferopsid or gnetalian types (cf. discussion in text).

Go: Ginkgoales, including *Baiera, Karkenia,* and *Ginkgo* (Permian?–Recent). We have excluded the Early Permian genus *Trichopitys,* considered a primitive ginkgo by Florin (1949), because of doubts raised by Meyen's (1984) interpretation of its axillary fertile structures as pinnate. However, our conclusions based on later groups are consistent with Florin's interpretation of *Trichopitys.* Czekanowskiales may be a derived subgroup (cf. Meyen, 1984), with the "bivalved capsules" representing fertile short shoots bearing two facing megasporophylls. A possible autapomorphy is the absence of sterile appendages on the axillary fertile shoots, but this is also seen in some early conifers (Florin, 1951).

Cn: Coniferales, including Lebachiaceae, Podocarpaceae, and Taxaceae (Late Carboniferous–Recent). Some *Podocarpus* species have compound male strobili (Wilde, 1944), which contrast with the compound female but simple male strobili of even the oldest and most primitive Lebachiaceae. This might suggest a relationship with cordaites (Beck, 1981), but the derived primary xylem pitting, endarchy, siphonogamy, and tiered proembryos of podocarps indicate that they are more closely related to conifers. Florin (1951) considered the terminal ovule of Taxaceae evidence against their derivation from a lebachiaceous prototype, but leaf morphology, wood anatomy (tertiary spiral thickenings), pollen morphology, and microgametophyte structure suggest relationships with Cephalotaxaceae, and hence secondarily terminal ovule position (cf. Crane, 1985a; Harris, 1976).

Autapomorphies include tiered proembryos and presence of compound female but simple male strobili (assuming that the conditions in *Podocarpus* and Taxaceae are secondary), which we interpret as representing a different pattern of aggregation from the compound male and female strobili in cordaites (see discussion of character 40). Crane (1985a) cites narrowly triangular leaves as an autapomorphy (assuming that the multiveined leaves of some podocarps and araucarians are secondary, as implied by Lebachiaceae), but this is questionably distinct from the condition in *Ephedra.* Crane points out that *Ephedra* differs in having opposite or whorled phyllotaxy and a basal sheath, but these are gnetalian apomorphies that would not preclude derivation from the conifer condition. Other autapomorphies cited by Crane are resin canals (although he notes that Pennsylvanian forms lack an epithelium, and the distinction between these and "mucilage canals" is uncertain, especially in fossil groups) and possibly only one plane of symmetry in the seed (Rothwell, 1982).

Ep: *Ephedra* (Early Cretaceous?–Recent). Striate "ephedroid" pollen of probable gnetalian affinities extends back to the Triassic, but earlier forms differ in various respects from pollen of extant *Ephedra* (twisted muri, presence of a sulcus, etc.). Autapomorphies include presence of only one or two flowers per female cone and possibly formation of the outer integument from lateral rather than anterior-posterior perianth parts (Martens, 1971; Takaso, 1985: see discussion of character 33–35).

We: *Welwitschia* (Recent). Some Early Cretaceous striate monosulcate pollen resembles *Welwitschia,* but this may be the basic pollen type for Gnetales as a whole. Obvious autapomorphies include the presence of only one pair of functional leaves, modification of the second pair to "scaly bodies," fusion of axillary buds into concentric ridges bearing reproductive shoots, and prothallial tubes (Martens, 1971).

Gn: *Gnetum* (Recent). Autapomorphies include fusion of the bracts of the compound strobilus into collars, multiple axillary flowers, the completely free-nuclear micropylar end of the mature megagametophyte, and possibly the multilacunar nodes with an even number of traces (Martens, 1971).

Ag: angiosperms (Early Cretaceous–Recent). Apparent autapomorphies are listed in the text (see also **Appendix III**). Some, particularly non-laminated endexine, megaspore wall without sporopollenin, and other embryological characters, could conceivably have existed in fossil groups where there is no information on the relevant organs. Another possible autapomorphy is trilacunar nodes, if this is basic in angiosperms.

Appendix II: Characters Used

Throughout, we use 0 for the presumed ancestral character state, 1 for the derived state, and X for missing information (coded 9 in PHYSYS, ? in PHYLIP). As discussed in the text, X is used in partially ordered multistate characters for states where the precursor state in unknown. When only one state is listed in the definition of a character, it is the derived state. Numbers of corresponding characters used by Hill and Crane (1982) and Crane (1985a) are indicated in parentheses; characters of these authors that we have not used are discussed in **Appendix III**. In a few cases, we mention implications of our cladistic analyses concerning the validity of assumptions made in our initial analysis of characters.

In addition to the references cited individually, several general works were consulted throughout for data on character distribution and are not cited below unless they conflict with other sources or otherwise merit special mention. These include Sporne (1965) and Stewart (1983) for all groups and the following for specific groups: *Aneurophyton, Archaeopteris*: Beck (1971, 1976), Scheckler and Banks (1971a, 1971b); *Pitus*: Gordon (1935), Long (1979); lyginopterids, *Medullosa*: Scott (1923), Stidd (1981), Taylor and Millay (1981); *Callistophyton*: Rothwell (1981); glossopterids: Gould and Delevoryas (1977), Pant (1977); *Peltaspermum*: Harris (1932a), Townrow (1960); corystosperms: Archangelsky and Brett (1961), Thomas (1933), Townrow (1962); *Caytonia*: Harris (1940, 1951); Bennettitales: Harris (1932b), Sharma (1977); *Pentoxylon*: Sahni (1948), Vishnu-Mittre (1953, 1957); Gnetales: Martens (1971).

BRANCHING

1. 0 = branching apical; 1 = axillary (Crane 9.8).

Studies of Scheckler (1978) and Beck (1979) on primary vasculature contradict earlier indications (Beck, 1970) that *Archaeopteris* had axillary branching. *Pitus* is known to have branched, but the exact mode of branching is unknown (Gordon, 1935; Long, 1979). The

scoring of *Heterangium–Lyginopteris* is based on *Lyginopteris* (Blanc-Louvel, 1966; Brenchley, 1913). According to Galtier and Holmes (1982), axillary branching in *Lyginopteris* differed from that in *Callistophyton* and modern plants in that the bundles to the branch do not connect to the sides of the "leaf gap" because of the long vertical course of leaf traces; however, they noted that the branch departs from the same level as the leaf and was presumably induced by it. Scoring of *Medullosa* is based on Hamer (pers. comm. cited by Crane, 1985a). Crane (1985a) followed the conventional description of cycads as having adventitious branching, but since (as he noted) modern developmental studies are lacking, we score them X. In our previous study (Doyle & Donoghue, 1986), we scored *Caytonia* X, but axillary branching is described by Harris (1971). Crane (1985a) assumed that *Peltaspermum* and corystosperms had axillary branching, but since no data exist, we score them X.

2. 0 — axillary buds single; 1 — multiple.

The derived state is apparently characteristic of all three genera of Gnetales (Bierhorst, 1971). In *Welwitschia*, Martens (1971) interpreted the "concentric ridges" on the crown as series of coalescent bases of buds axillary to the two leaves.

LEAF DISTRIBUTION AND ARRANGEMENT

3. Leaves on (homologs of) progymnosperm penultimate order branches.

This is an advance of *Archaeopteris* over Aneurophytales, which have leaves on the last-order branches only. If coniferopsids are derived directly from progymnosperms, they have the *Archaeopteris* condition (this is especially clear if one compares the leafy branch systems of conifers and *Archaeopteris*: Beck, 1971). We assume that this change did not occur in the ancestry of seed ferns; if pteridophylls correspond to whole progymnosperm branch systems and pinnules to progymnosperm sphenophylls, pteridophylls derived from archaeopterid rather than aneurophytalian branch systems would presumably have pinnules interpolated between pinnae on the rachis, but such rachial pinnules are lacking in most Carboniferous seed ferns (including the more primitive ones).

Since we wished to allow for the possibility that pinnately organized simple leaves are derived from several sources (cf. character 5–7), they are coded X for this character. In ginkgos and cordaites, it is not clear what would correspond to particular orders of vegetative branching in progymnosperms. However, we have scored them 1, based on the presence of bracts on the axes bearing the fertile short shoots, which would correspond to penultimate order axes in *Archaeopteris*.

4. 0 = phyllotaxy spiral; 1 = opposite-decussate or whorled.

Opposite-decussate phyllotaxy occurs in some progymnosperms (*Tetraxylopteris*, *Proteokalon*: Scheckler & Banks, 1971b) and one medullosan (*Quaestora*: Mapes & Rothwell, 1980), but these were not included in the analysis (see **Appendix I**) and are most likely independent derivations.

LEAF ARCHITECTURE

5–7. 000 = simple, dichotomous leaves only; 100 = pinnately compound leaves and cataphylls; 110 = once-pinnate or simple pinnately veined leaves and cataphylls; X01, XX1 = pointed cataphyll-like leaves only, or simple, linear or dichotomous leaves (with parallel or divergent venation) and cataphylls.

000, X01, and XX1 correspond to the ancestral state of Crane 9.11; 100 and 110 to the derived state.

See text for discussion.

8. 0 = rachis regularly bifurcate; 1 = usually or always simple.

The ancestral status of the bifurcate rachis is based on its ubiquity in primitive seed ferns; it is not strongly supported by outgroup comparison, although one aneurophyte, *Proteokalon*, does have forked branch systems (Scheckler & Banks, 1971b). This character applies only to pteridophylls; groups with simple leaves are scored X, since we are agnostic on their origin. Although we scored *Caytonia* as pinnately compound (character 5–7), we scored it X for this character because its leaves are so simplified that any assumptions regarding the rachis condition in its ancestors seem unjustified.

Stidd and Hall (1970) considered the simple rachis to be a diagnostic character of Callistophytaceae. Rothwell (1975) described one case of a bifurcate rachis in *Callistophyton*, but most of the young leaves that he saw had a simple rachis. Since the shift to a simple rachis seems nearly complete, it seems more informative to group this mixed condition with the non-bifurcate state rather than the prolifically bifurcating state seen in most Carboniferous seed ferns.

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 the finest order reticulate.

Hill and Crane's character 5 differs (and is ambiguous) in distinguishing 1–2 orders of venation and 2 or more orders; they score only *Gnetum* and angiosperms as derived.

This character is redefined somewhat from our previous study (Doyle & Donoghue, 1986), where 10 designated only one order of reticulate venation and 11 designated several orders. This leads to a change in the scoring of *Welwitschia* (from 10 to 11), which recognizes that *Welwitschia* leaves differ from others with parallel-dichotomous venation in having both anastomoses and interpolated finer veins. Both formulations see the presence of reticulations as potential evidence of relationship between angiosperms and simply reticulate forms such as *Caytonia* or glossopterids.

EPIDERMAL ANATOMY

11. 0 = poles of guard cells raised; 1 = level with aperture.

Scoring of most groups is based on Harris (1932a), or on descriptions and figures in Florin (1931), Townrow (1962), and Reihman and Schabilion (1976). Harris (1932a) stated that guard cells of peltasperms are flat, but this was based on one abnormal stomate on the upper leaf surface, so we have scored them X. According to G. R. Upchurch (pers. comm.), close examination shows that the guard cell poles of *Gnetum* are raised.

12. 0 = stomata entirely haplocheilic; 1 = some or all syndetocheilic.

Most data are from Florin (1931) and general references on groups. The condition in progymnosperms is unknown, but polarity seems clear from the ubiquity of haplocheilic stomata in seed ferns and coniferopsids. The term syndetocheilic implies both paracytic mature topography and mesogenous development; perhaps the latter is more fundamental, but in practice only the former is usually demonstrated, particularly in fossils. Oestry-Stidd and Stidd (1976) reported syndetocheilic stomata in medullosans, but Reihman and Schabilion (1978) argue that this was a misinterpretation, and Stidd (1981) accepts that this is possible. *Pentoxylon* was originally described as syndetocheilic but seems to be haplocheilic, based on Vishnu-Mittre (1957) and Douglas's (1969) account of *Taeniopteris* leaves from Australia, which are probably pentoxylalian (Drinnan & Chambers, 1985). Maheshwari and Vasil (1961) rejected earlier claims that *Gnetum* is syndetocheilic, arguing that some stomata

have haplocheilic development. However, other stomata that they figured are paracytic (about 90% of those on a leaf, according to Upchurch, pers. comm.), and on the basis of more detailed ontogenetic studies, Nautiyal et al. (1976) reaffirmed that *Gnetum* stomates are mesogenous and argued that non-paracytic stomates are the result of secondary divisions. Based on studies of Early Cretaceous and modern leaves, Upchurch (1984) proposed that the basic condition in angiosperms is mixed (both topographically and developmentally). We defined the character so as to include these mixed conditions with purely syndetocheilic, since it is unclear which is more derived, and since syndetocheilic is such a departure from the basic condition in seed plants that it seems justified to consider any expression of it as potential evidence of relationship.

APICAL MERISTEM

13. Apical meristem with differentiation of tunica and corpus (Hill and Crane 2).

We assume that the tunica of Araucariaceae is derived within conifers (Sporne, 1965).

STELE

14, 15. 00 = protostele (including vitalized types); 10 = eustele usually with external secondary xylem only; X1 = eustele with regular internal secondary xylem.

States 10 plus X1 correspond to Crane 9.1.

In coding this character, our first priority was to reflect the concept that the eustele of *Medullosa* (Basinger et al., 1974) probably originated directly from a protostele rather than a regular eustele. This is based on its peculiar internal secondary xylem and arc-like primary xylem strands and the existence of allied protostelic forms (*Quaestora, Sutcliffia*, not included in our analysis). Coding eustele and internal secondary xylem as two characters would add a step to the origin of *Medullosa*, which would conflict with this line of reasoning. Crane (1985a) also accepts these arguments, but his solution is to treat the protostelic and eustelic medullosans together and to score them as protostelic. This has the disadvantage of leaving unexpressed the similarity between *Medullosa* and later forms with internal secondary xylem, particularly corystosperms (accepting that their stem was *Rhexoxylon*, which was originally assumed to be a medullosan: Archangelsky, 1968; Bancroft, 1913). For this similarity to be relevant, medullosans as usually defined would have to be paraphyletic, but this is entirely possible (see Appendix I).

Our decision to code the normal eustele 10 and the *Medullosa*-type eustele X1 rather than vice versa was a difficult one. Both solutions allow for direct derivation of the *Medullosa*-type eustele from a protostele, but both produce undesirable biases. The alternative coding, which we used in our previous paper (Doyle & Donoghue, 1986) and preliminary analyses in the present study, sometimes has the effect of favoring origin of normal eusteles in general from the *Medullosa* type. This agrees with the hypothesis that cycads were derived from medullosans, as suggested by the fact that there is a trend to elimination of internal secondary xylem in Permian medullosans, resulting in cycad-like stems, but it seems less plausible as a general phenomenon on both anatomical and stratigraphic grounds. Thus in our previous analysis cycads were linked with *Medullosa*, but when the same coding was used with the present data set, the most parsimonious trees obtained were of one of the types in Figure 5b, with corystosperms basal in platysperms. As discussed in the text, this implies that all higher seed plants with normal eusteles and unilacunar nodes were ultimately derived from ancestors with *Medullosa*-type steles and multilacunar nodes, and it entails a long gap in the record of the corystosperm line. Conversely, the present coding produces a subtle bias in favor of general derivation of *Medullosa*-type steles from normal eusteles. This has some disadvantages but seems more plausible in the majority of cases. Thus it has the effect of

implying that *Medullosa* and cycads had a common ancestor with a normal eustele in trees where the two groups are linked (Fig. 5e), which seems unlikely in view of the existence of protostelic medullosans. However, the idea that internal secondary xylem arose after the eustele is borne out for *Pentoxylon* in all trees obtained, and it makes more sense for corystosperms, considering their age and advanced seed and pollen features indicating relationships with other platysperms.

Occasional internal secondary xylem occurs in *Pitus*, associated with branching (Long, 1979), and in *Lyginopteris*, where Scott (1923) suggested that it is related to injury. Some tendency may thus be primitive in seed ferns, but regular presence seems a definite advance.

Crane (1985a) scores fossils in which stem anatomy is unknown as eustelic, but we consider XX the only justifiable scoring. Our scoring of "higher lyginopterids" as protostelic does not conflict with Crane's scoring of *Lyginopteris* as eustelic, since our taxon includes *Heterangium* as well as *Lyginopteris*. Scoring of glossopterids is based on *Araucarioxylon arberi* (firmly associated with glossopterids by Gould, 1975), which has a pith with no internal secondary xylem (Beeston, 1972), and on the fact that none of the Gondwanian Permian woods described by Maheshwari (1972) have internal secondary xylem.

16. 0 = some or all stem bundles mesarch or exarch; 1 = all endarch (roughly Hill and Crane 46).

Stem bundles that give rise to leaf traces in the cordaite *Mesoxylon* are mesarch, although other bundles in *Mesoxylon* and all bundles in other genera are endarch. This partial retention of the mesarch condition is generally considered a primitive feature of cordaites. In order to stress the fact that conifers and ginkgos are distinctly more advanced in this character, we have included the cordaite condition in the primitive state.

In our previous paper we followed Sahni (1948) and Vishnu-Mittre (1957) in scoring *Pentoxylon* as mesarch, but since Sahni remarked that the primary xylem is so poorly preserved as to leave doubt, we have rescored it X. Pennsylvanian conifers (Rothwell, 1982) and Triassic cycads (Gould, 1971) are like modern members in being endarch.

NODAL ANATOMY

17, 18. 00 = leaf traces from one stem bundle or protoxylem strand ("one-trace unilacunar"); 10 = from more than two bundles ("multilacunar"); X1 = from two adjacent bundles ("two-trace unilacunar").

In our previous paper, we treated nodal anatomy as a simple binary character and scored forms with leaf traces from one stem bundle and from two adjacent bundles as 0, because of uncertainty on the relationships among the various character states. However, comparison with progymnosperms and lyginopterid seed ferns indicates that supply from one bundle is primitive, and there is no reason to suspect that the two-trace condition was an intermediate step on the way to the multilacunar condition (except in *Gnetum*, which differs from other multilacunar groups in having an even number of traces: Martens, 1971). On the other hand, preliminary indications on relationships of two-trace groups suggest that origins from both one-trace and multilacunar are possible, so X1 is the appropriate coding.

In corystosperms (*Rhexoxylon*), Archangelsky and Brett (1961) stated that leaves are supplied by traces from at least 3–4 gaps, some at different levels. Like modern cycads, the Triassic genus *Lyssoxylon* (Gould, 1971) has several girdling leaf traces, which we interpret as a special case of multilacunar. The situation in *Welwitschia* is confusing but seems most readily interpreted as a variant on the two-trace condition (Martens, 1971). In angiosperms, we follow Takhtajan (1969) rather than Bailey (1956), who considered "two-trace, unilacunar" nodes primitive; as noted by Benzing (1967), this condition is closely associated with opposite phyllotaxy, a presumed derived character in the group.

Leaf bases suggest that *Peltaspermum* had two veins in the petiole (Meyen, 1984; Townrow, 1960), while *Caytonia* leaf scars show a simple arc (Harris, 1964); this suggests two-trace and one-trace conditions, respectively, but because bundles can split or fuse in the cortex, we have scored both taxa XX. Although the nodal anatomy of glossopterids has not been described, we scored them 0 (one- or two-trace) in our previous paper, since all the Gondwanian woods described by Maheshwari (1972) have a *Callistophyton*- or coniferopsid-like aspect that contrasts with the more manoxylic construction of known multilacunar groups. However, this extrapolation was probably unjustified and certainly cannot be used now that we distinguish three nodal conditions. Hence we have rescored glossopterids XX.

WOOD ANATOMY

19. 0 = some scalariform pitting in metaxylem; 1 = no scalariform metaxylem, isolated circular bordered pits in protoxylem (Hill and Crane 8 plus 9).

This corresponds to the ordinary vs. coniferophyte types of Bierhorst (1971). Absence of scalariform pitting is associated with presence of circular bordered pits in the protoxylem and vice versa in all cases where both tissues are known; hence we combine the two characters.

Polarity seems well established on outgroup comparison with ferns and sphenopsids and the presence of scalariform metaxylem in aneurophytes (Scheckler & Banks, 1971a) and *Archaeopteris* (*Callixylon newberryi*: Beck, pers. comm., contrary to Beck, 1970). *Heterangium*, *Lyginopteris*, and *Medullosa* have circular pitting in the internal metaxylem, but "spiral or scalariform" in tracheids immediately outside the protoxylem (Scott, 1923); scalariform pitting also occurs in leaf traces of *Heterangium* (Jennings, 1976) and *Medullosa* (Scott, 1923). In *Callistophyton*, Rothwell (1975) stated that the metaxylem has "reticulate-bordered" pitting, but he cited "spiral-scalariform" in the protoxylem; the latter may include some metaxylem, since the pits in his figures seem to show borders. Pant and Singh (1974) reported some scalariform pitting in *Glossopteris*; they were not sure whether the xylem concerned was primary or early secondary (cf. the transitional scalariform xylem of *Cordaites*), but the definite secondary xylem tracheids that they showed are all circular bordered. *Rhexoxylon* (corystosperms) has irregular spiral or scalariform pitting in both centripetal and centrifugal metaxylem (Archangelsky & Brett, 1961). *Pentoxylon* has scalariform metaxylem pitting (at least in the short shoots); protoxylem is not described (Vishnu-Mittre, 1957).

20. 0 = only circular bordered pitting or perforations in secondary xylem; 1 = at least some scalariform.

Scalariform secondary xylem pitting in angiosperms has been considered a primitive feature precluding derivation of angiosperms from most gymnosperm groups (Takhtajan, 1969), but this is based on a questionable comparison with the primary xylem of ferns. Instead, its absence in progymnosperms (except *Protopteridium*, a possible basal lignophyte taxon not included in our analysis) and Paleozoic seed plants suggests that it is derived (cf. Beck, 1970). In cycads, scalariform secondary xylem occurs only in *Zamia* and *Stangeria*, presumably advanced genera (cf. Crane, 1985a); it is not reported in Triassic forms (Archangelsky & Brett, 1963; Gould, 1971). The condition in Bennettitales varies (even among species of *Bucklandia*: Bose, 1953; Nishida, 1969), but in view of the widespread occurrence of scalariform pitting we have provisionally scored them as 1. Contrary to earlier reports, *Pentoxylon* has some scalariform as well as circular bordered pitting (Vishnu-Mittre, 1957). We assume that the scalariform pitting of cordaites is irrelevant, since it occurs only at the transition between the primary and secondary xylem. Previously (Doyle & Donoghue, 1986) we scored *Gnetum* 1, based on the report by Muhammad and Sattler (1982) of scalariform

perforations in its vessels, but because there is no evidence on whether this is basic within the genus, we have rescored it X.

21. Vessels in the secondary xylem (Hill and Crane 7, Crane 9.32 in part).

Angiosperms are scored X in order to allow for the possibility that the vesselless condition is either primary (the conventional view) or secondary (Young, 1981). Crane (1985a) qualifies the definition to "vessels with porose perforation plates" to exclude angiosperms, but especially considering Muhammad and Sattler's (1982) report of scalariform perforations in *Gnetum*, we prefer to leave the question of comparability open.

22. 0 = rays uniseriate or rarely biseriate; 1 = at least some multiseriate.

We assume that multiseriate rays in progymnosperms (*Tetraxylopteris*, *Callixylon newberryi*: Beck, 1957, 1970) arose within the group. Rothwell (pers. comm.) reports that some cordaites (*Mesoxylon*) have multiseriate rays, but judging from most descriptions this is exceptional and of uncertain significance. Bennettitales are marginal (1–2-seriate in *Cycadeoidea*, 1–3-seriate in *Bucklandia*: Bose, 1953); we assume that the presence of some multiseriate rays is basic. Contrary to earlier reports, *Pentoxylon* has occasional bi- and multiseriate as well as uniseriate rays (Vishnu-Mittre, 1957). Our scoring of *Welwitschia* is based on a section provided by R. Schmid of a root with a few tiers of secondary xylem tracheids.

SECRETORY STRUCTURES

23. Secretory canals.

In our previous paper, we also recognized secretory cavities (as in *Callistophyton*, corystosperms, cordaites, and *Ginkgo*) as 10 in a three-state character, with no secretory structures coded 00 and canals X1, but we now feel that this was premature. Our coding assumed that cavities might or might not be precursors of canals, but that canals were less likely to become cavities; however, there is little anatomical or preliminary phylogenetic support for this assumption. Furthermore, anatomical definition of cavities is vague, and they are not always clearly distinguished from mucilage cells, which occur, for example, in the pith of *Pitus* and the cortex of putatively associated *Tristichia* (Gordon, 1935; Long, 1961). Hence we now recognize only canals, which are more distinctive. We have not distinguished between mucilage and resin canals, in order to allow for the possibility that one is derived from the other, and because the two cannot be distinguished in fossils.

Gould and Delevoryas (1977) show no secretory structures in leaves or fructifications of *Glossopteris*, but many of the Gondwanian woods described by Maheshwari (1972) have "secretory cells" or "canals" in the pith; since some (or most) of these are probably glossopterids, it seems prudent to score the group X. "Resin" canals occur in Middle Pennsylvanian conifers (Rothwell, 1982). *Pentoxylon* cortex contains sclerotic nests but no secretory structures (Sahni, 1948; Vishnu-Mittre, 1957). There are no canals in *Ephedra*, and resin is unknown in Gnetales, but lysigenous mucilage canals occur in *Welwitschia* (Martens, 1971).

CHEMISTRY

24. Mäule reaction (Hill and Crane 45).

An indication of substantial proportions of syringaldehyde (syringyl) as well as vanillin (guaiacyl) units in the lignin (Gibbs, 1957; Gottlieb & Kubitzki, 1984). There are exceptions in conifers (*Tetraclinis*, some species of *Podocarpus*), but these seem clearly derived within the group. Several cycads show a reaction in the stomata and/or fibers, but because these

do not include *Cycas* (presumably basal in cycads) and no reaction is seen in the xylem (Gibbs, 1957), we score them 0.

MORPHOLOGY OF FERTILE APPENDAGES

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.

X01 and XX1 for microsporangiate structures correspond roughly to Hill and Crane 47 (stalked vs. laminar microsporangia), but as noted below we score some groups differently. In most respects, this system parallels our coding of the leaf character (5–7). A difference is that the 110 state is restricted to once-pinnate sporophylls, with leaflets or potentially homologous cupules or stalks bearing clusters of pollen sacs arranged pinnately along a rachis. This excludes cycads, which have pinnately organized but simple sporophylls, with ovules evenly spaced along either side of the rachis and abaxial pollen sacs scattered on either side of the midrib of a scale-like structure. We did score cycads 110 in our previous paper (Doyle & Donoghue, 1986), but their sporophylls are so different from others scored 110 that it seems unwarranted to assume that they passed through a once-pinnate intermediate state. The alternative, that they were reduced directly from pinnately compound along a different pathway, might in fact be suspected on stratigraphic grounds, since if Pennsylvanian *Spermopteris* and Permian taeniopterids are cycads (Mamay, 1976), they appear before any groups with once-pinnate sporophylls (except glossopterids). Our solution is to score cycads 1X0, which treats derivation from pinnately compound (100) or once-pinnate (110) as equally likely.

We interpret the three-dimensional cupulate structures and pollen organs (*Telangium*) borne at the bifurcation of the frond in Early Carboniferous seed ferns (including *Pitus* as reconstructed by Long, 1963, 1979) as a retention of the progymnosperm condition; not specifying that the fertile branch is part of a frond represents only a slight loss of information.

We interpret the fertile structures of *Caytonia*, peltasperms, and corystosperms as pinnate sporophylls, but it has also been suggested that they were branch systems (Stebbins, 1974; Thomas, 1933; see text for further discussion). The foliar interpretation is best supported by the dorsiventrality of the cuticle on the main axis in ovulate and pollen structures of *Caytonia* (Harris, 1940, 1951) and peltasperms (Townrow, 1960) and the pollen structures of corystosperms (Townrow, 1962). The ovulate structures of corystosperms need reinvestigation, but the lack of a regular relationship between the so-called "bracts" and "secondary axes" suggests that they are better interpreted as reduced rachial pinnules and pinna rachises, respectively (Harris, 1951). Townrow (1960) indicated that microsporophylls of peltasperms (*Antevsia*) are bipinnate, since each "paddle" has several groups of pollen sacs. In corystosperms, however, pollen sacs are scattered evenly on each paddle (Townrow, 1962), so we score them 110.

A special case concerns the glossopterids, which have multiveined cupule-like structures or aggregations of pollen sacs attached singly or pinnately to the adaxial surface of a leaf-like structure (Gould & Delevoryas, 1977; Retallack & Dilcher, 1981). Like Crane (1985a), we assume that the pinnate arrangement, as in the pollen organs and the ovulate organ *Lidgettonia*, is the basic condition. A variety of hypotheses can be envisioned for the homologies of these structures; some are discussed by Retallack and Dilcher (1981), others in the text. Under two interpretations, that the adaxial fertile structure is a once-pinnate

sporophyll fused to a leaf or an axillary branch bearing one such sporophyll, the appropriate scoring would be 110, with the axillary position considered a separate character (presumably an autapomorphy). This has the advantage of being the same as the scoring of angiosperms, which is consistent with the view of Stebbins (1974) and Retallack and Dilcher (1981) that the whole ovulate structure could be converted into a carpel with no change in positional relationships. Under another interpretation, that the fertile structure is an adaxially oriented portion of a compound leaf, analogous to the fertile segment in the fern family Ophioglossaceae, a more appropriate coding might be 100, which would allow for reduction from a compound frond along different lines from groups scored 110. A final possibility, that the adaxial structure is an axillary branch bearing simple sporophylls, seems best scored as 000, since the cupules themselves have flabellate venation (Schopf, 1976) and are hence more comparable to the fertile appendages of progymnosperms (000) than the one-veined sporophylls of coniferopsids (X01). This coding would not rule out homology with the axillary fertile short shoots of coniferopsids (Schopf, 1976), but it adds a step between them, as it should: either glossopterids are one step more primitive than coniferopsids in retaining dichotomous venation of the sporophylls, or they are secondarily elaborated. The coding adopted, XX0, covers all these possibilities, besides highlighting the morphological uncertainties.

Ovulate receptacles of Bennettitales and *Pentoxylon* are most simply interpreted as axes with secondarily reduced, stalk-like megasporophylls (Chamberlain, 1935). A less plausible alternative is that the receptacle is a secondarily terminal, radial megasporophyll, perhaps analogous to the three-dimensional pollen organs of *Pentoxylon*, and the stalks are cupule (leaflet) homologs, as suggested for the whole bennettitalian flower by Delevoryas (1968). Crane's (1985a) coding, as "unicupulate" megasporophylls, biases toward derivation from seed fern sporophylls with cupules. Bennettitales seem to have normal planated microsporophylls, but it is unclear whether they are basically bipinnate or once-pinnate. We assume that once-pinnate is basic, since, as noted by Harris (1932b), this is the condition seen in all early Bennettitales, while bipinnate sporophylls appear late in the history of the group and in otherwise advanced members (*Williamsonia spectabilis*, Middle Jurassic; *Cycadeoidea*, Late Jurassic–Cretaceous). (Harris himself hesitated to question the view, based on comparison with Paleozoic seed ferns, that bipinnate is primitive.) Pollen organs of *Pentoxylon* are a special case: they are reported to be three-dimensional, with numerous spirally arranged stalked microsporangia (Vishnu-Mittre, 1953), but they are whorled and basally fused, like bennettitalian microsporophylls, which suggests that they are appendicular. We have coded them 010, which puts them one step from a once-pinnate sporophyll (loss of bilateral character) or from a branch with simple microsporophylls (conversion to appendicular status).

As with the leaf character, coniferopsids are scored X01, so that they are one step removed from seed ferns and progymnosperms but two from groups with once-pinnate sporophylls, while Gnetales are scored XX1, so that they are also only one step from groups with once-pinnate sporophylls, such as Bennettitales (see discussion of the leaf character in the text for rationale).

We have followed Florin's (1949) interpretation of ginkgo reproductive structures as coniferopsid-type axillary shoots bearing simple sporophylls, rather than axillary pinnate organs, as proposed for *Trichopitys* by Meyen (1984). The microsporangiate cones in modern *Ginkgo* show no sign of dorsiventrality, and Cretaceous *Karkenia* has axillary ovulate structures bearing numerous ovules on all sides (Archangelsky, 1965).

In scoring angiosperms, we have interpreted carpels as once-pinnate, with the bitegmic ovules potentially homologous with cupules of Mesozoic seed ferns (cf. Crane, 1985a; Doyle, 1978; Gaussen, 1946; Stebbins, 1974). Hill and Crane (1982) scored angiosperms as having stalked (vs. laminar) microsporangia, like conifers and Gnetales. However, stalk-like stamens in angiosperms have been considered advanced relative to the laminar types of some mag-

noliids. Furthermore, the bilateral character of angiosperm stamens, with a pair of pollen sacs on either side of the connective, suggests that they are basically pinnate structures. Hence we score angiosperm stamens too as 110.

31. 0 = ovule on lateral appendage; 1 = terminal.

Eames (1952) claimed that *Ephedra* ovules are appendicular (pseudoterminal) and hence different from the terminal ovules of *Welwitschia* and *Gnetum*, but this was based on questionable analogies with the male cones and on vascular and ontogenetic arguments not supported by more recent observations (Martens, 1971; Takaso, 1985). In any case, Eames did not establish that *Welwitschia* and *Gnetum* have truly terminal ovules by the same criteria, and even if they do, it seems unwarranted to assume that they could not have been derived from ancestors with the *Ephedra* condition.

32. 0 = homologs of progymnosperm fertile branchlets on homologs of lower order axes; 1 = on homologs of last order axes.

This character expresses a change from the aneurophytalian condition, where dichotomous fertile appendages are borne on penultimate order axes, replacing vegetative branches, to that in *Archaeopteris*, where they are borne on last order axes, replacing leaves. If coniferopsids are directly derived from progymnosperms, they have the *Archaeopteris* state, since their fertile appendages are borne on last order axes, in the same spiral with scale leaves. As with character 3, we have assumed that this change did not occur in the ancestry of groups with pinnately compound mega- and/or microsporophylls, based (somewhat speculatively) on the morphological correspondence between fertile appendages of aneurophytes and the cupulate systems of early lyginopterids (e.g., *Pitus* as reconstructed by Long, 1979), which were borne on an apical continuation of the rachis, more like pinnae than pinnules. We have scored groups with basically once-pinnate sporophylls only (cycads, Bennettitales, angiosperms) and Gnetales as X, since we do not wish to assume whether their sporophylls are derived from simple or compound structures.

CUPULES, OUTER INTEGUMENTS

33–35. 000, 010 = ovule(s) in radial cupule; 100 = ovules directly on more or less laminar sporophylls; 110 = ovules in anatropous (circinate) cupules, or anatropous and bitegmic; X01 = ovule with second "integument" derived from two appendages lower on axis.

Crane 9.19 corresponds roughly to 110 plus 010 (except that he scores glossopterids as derived), Crane 9.24 to 010.

Radial cupules of Carboniferous "lyginopterids" are considered primitive in seed plants, based on their similarity in form and position to the dichotomously organized fertile appendages of progymnosperms. Presumably ovules correspond to the groups of sporangia on such appendages, with the outer sporangia sterilized to form the integument around one remaining sporangium. In our previous paper (Doyle & Donoghue, 1986) we scored progymnosperms XXX for this character, but based on this comparison we now score them 000.

Seed ferns with non-cupulate ovules borne on relatively unmodified leaves are coded 100. This is consistent with any of the likely mechanisms for loss of the original lyginopterid cupule in medullosans, *Callistophyton*, and other groups: reduction, transformation into a new integument after reduction of the ovules to one (Meyen, 1984; Walton, 1953), or dedifferentiation from the rest of the frond.

Coding of other states has been changed from Doyle and Donoghue (1986). There we

coded strongly reflexed (anatropous, circinate) cupules X10, which allows them to be derived by one step either from lyginopterid cupules by recurvation or from leaflets bearing laminar ovules by enrollment. Ovules in glossopterids are also somewhat enclosed by a cupule and were coded the same as anatropous forms by Crane (1985a), but since the cupule is folded involutely, not tip to base, we scored them 100. We scored Bennettitales the same as lyginopterids (000), based on presence of a radial cupule in *Vardekloeftia* and *Bennetticarpus crossospermus* (Crane, 1985a; Harris, 1932b, 1954). In Gnetales, the terminal ovule is surrounded by an additional layer; its development (from two primordia lower on the axis: Martens, 1971; Takaso, 1985) and positional relationships suggest that this "outer integument" corresponds to the perianth below the whorl of microsporophylls in the male flower. This means that if Gnetales are derived from forms like Bennettitales, they must have lost the cupule (whether by reduction or fusion with the true integument), whereas no such loss would be required if they are derived from coniferopsids (Eames, 1952). With these considerations in mind, we coded Gnetales 101, which put them two steps from Bennettitales (loss of the cupule and modification of the perianth into the outer integument) and one from coniferopsids (formation of the outer integument from sterile appendages of the fertile short shoot).

We were forced to modify this scheme as a consequence of accepting Crane's (1985a) conclusion that *Pentoxylon* had a cupule. This was based on Harris's (1962) description of pentoxylalian seeds from New Zealand, which showed that the supposed sclerotesta has a separate cuticle from the sarcotesta, suggesting two morphologically distinct envelopes are present, as in *Vardekloeftia*. We realized that rescoring *Pentoxylon* 000 would indirectly bias against Crane's hypothesis that angiosperms, Bennettitales, *Pentoxylon*, and Gnetales are all derived from seed ferns with anatropous cupules, since under that hypothesis two or more X-coded taxa would be placed between taxa with other codings on the cladogram, thus introducing the bias associated with X-coding explained in the text. Eliminating this bias requires bolder assumptions on morphological relationships, but we believe that some such assumptions can be made without excessive speculation.

The basic change that we made was to recode anatropous cupules as 110. This places them two steps from lyginopterid cupules rather than one, thus favoring the hypothesis that they are leaflets. This bias seems acceptable in light of our preliminary analyses, in which groups with anatropous cupules were never closely associated with lyginopterids, but rather with groups with seeds borne directly on leaves (cycads, medullosans, or the platyspermic clade).

This required recoding bennettitalian cupules, since continuing to code them 000 would mean that two steps were required to derive them from anatropous cupules, whereas only one morphological change (a shift in orientation) would really be needed. We ran the analysis separately with two codings, 0X0 and 010, both of which meet the requirement of being only one step from anatropous, before deciding that the potential biases of 010 are less likely to be serious in practice. The greatest disadvantage of 0X0 is that it places only one step between the bennettitalian and gnetalian conditions, which conflicts with our morphological analysis of Gnetales. 010 introduces a new step between Bennettitales and lyginopterids, but this seems acceptable, since none of our preliminary analyses associated the two groups, despite their identical scoring in this character. 010 also has the disadvantage of placing two steps between Bennettitales and groups scored 100 (e.g., cycads). This biases in favor of derivation of the bennettitalian cupule from an anatropous one, as postulated by Crane (1985a), rather than de novo, and thus favors arrangements in which angiosperms are placed between groups coded 100 and Bennettitales. It seems reasonable to prefer derivation of structures from pre-existing ones over de novo origin; however, under arrangements with angiosperms between groups scored 100 and Bennettitales, the angiosperm outer integument

must itself originate de novo. We concluded that this bias was acceptable, since the same arrangement of taxa was obtained with both scorings of Bennettitales. However, extra steps due to this coding were encountered in some of our experiments, as discussed in the text.

We recoded the gnetalian condition X01, which still puts Gnetales one step from coniferopsids and two from Bennettitales, as desired. An undesirable feature is that Gnetales are now only one step removed from lyginopterids, but this is not a serious problem, since the two groups were never associated in our analyses. In general, we agree with Crane's (1985a) interpretation of gnetalian flowers, except that he accepts Eames's (1952) view that the outer integument of *Ephedra* consists of an anterior-posterior pair of bracteoles, whereas more recent ontogenetic and vascular data indicate that it consists of lateral bracteoles (Martens, 1971; Takaso, 1985). Both male and female flowers of *Welwitschia* have two perianth pairs, with the inner, anterior-posterior pair forming the outer integument; presumably the perianth of *Ephreda* corresponds to the outer pair. *Gnetum* has two outer integuments; we assume that these correspond to the two perianth pairs in *Welwitschia*, but it is conceivable that the inner one is homologous with the bennettitalian cupule. There are two nubs at the base of the abortive ovule in the male flower of *Welwitschia* (Martens, 1971) that might also be vestiges of the cupule; another intriguing possibility is that they are vestigial interseminal scales. Because these observations raise doubt as to whether the outer integument is a valid synapomorphy of the three genera of Gnetales, it might have been better to score them X00 for this character.

We also recoded coniferopsids, which have stalked or sessile non-cupulate ovules. In our earlier study they were coded 100, the same as *Callistophyton* (this seems appropriate, since they differ primarily in radical reduction of the sporophyll, coded elsewhere), but one step removed from *Archaeopteris*. However, the change from an *Archaeopteris*-like prototype is already implicit in the sporophyll character (reduction of a dichotomous appendage to a simple stalk), and this redundancy would bias against the Beck hypothesis. Hence we have recoded coniferopsids as X00, which is equivalent to saying that we do not know whether they once had a cupule and lost it (the case if they are derived from seed ferns) or never had one. To allow for the possibility that glossopterids are coniferopsids (Schopf, 1976), they too are rescored X00.

We have followed the conventional hypothesis that anatropous, bitegmic ovules are basic in angiosperms (e.g., Cronquist, 1968; Stebbins, 1974; Takhtajan, 1969), based on their near-ubiquity among magnoliids (with the notable exception of the orthotropous Piperales, including Chloranthaceae). Since such ovules are essentially identical to anatropous cupules (assuming that they are oriented the same way: see text), they are coded 110.

36. 0 = several ovules per anatropous cupule or potential homolog; 1 = one.

This corresponds partly to Crane 9.22 (uniovulate "cupule"), but differs in including possible non-anatropous homologs (leaflets bearing laminar ovules, as in glossopterids and peltasperms). The latter serve to polarize the character in anatropous groups, since they are all multiovulate. Bennettitales and *Pentoxylon* are scored X, since there are several hypotheses concerning the homology of their cupules.

MICROSPORANGIA

37. 0 = microsporangia terminal, marginal, or adaxial; 1 = abaxial.

Marginal and adaxial can be lumped, since adaxial is definitely known only in Bennettitales. Angiosperms may be a second case, since abaxial, marginal, and adaxial pollen sacs all occur in putatively primitive taxa. However, the basic condition is uncertain (cf. Takhtajan, 1969), so we score angiosperms X.

Previously (Doyle & Donoghue, 1986) we scored *Aneurophyton* X for "not applicable,"

since it was homosporous, but we now score it 0, since there is no question that its terminal sporangia are homologous with the microsporangia of other groups. *Lyginopteris* probably had *Crossotheca-Feraxotheca*-type pollen organs with abaxial pollen sacs (Taylor & Millay, 1981), but *Heterangium* and early lyginopterids are associated with *Telangium*-type structures, with terminal microsporangia (Jennings, 1976; Long, 1963, 1979), so we score both lyginopterid groups 0. In peltasperms and corystosperms, Townrow (1960, 1962) assumed that the pollen sacs are abaxial. In our previous paper we scored *Caytonia* the same, as it is usually illustrated (e.g., Crane, 1985a), but since Harris (1951) points out that orientation is actually unknown, we now score it X; in any case, the synangia are attached almost apically on the pinna equivalents. In our first paper we scored ginkgos 1, based on modern *Ginkgo*, but fossil *Baiera* has several radiating pollen sacs; since the basic condition is unclear, it seems best to score them X.

38. 0 = microsporangia free; 1 = fused at least basally into microsynangia.

Our scoring of multiovulate lyginopterids as 1 is based on *Telangium affine* (associated with *Pitus* by Long, 1979). *Heterangium* is also associated with *Telangium*, with 8 sporangia per synangium (Jennings, 1976). Peltasperms and corystosperms have free, unilocular pollen sacs (Townrow, 1960, 1962).

The isolated unilocular microsporangia of *Pentoxylon* and *Gnetum*, both highly advanced groups, are probably the result of reduction. Since it seems inappropriate to equate this with (or assume it was preceded by) secondary freeing of the sporangia, both groups are scored X.

ARRANGEMENT OF FERTILE STRUCTURES

39. 0 = microsporophylls spirally arranged; 1 = whorled.

This character is partly comparable to Crane 9.23, microsporophylls forming "flowers," which includes angiosperms. However, Crane's character seems too vaguely defined (see also **Appendix III**). The whorled arrangement in Bennettitales, *Pentoxylon*, and Gnetales is a more distinctive advance.

Crane scores *Gnetum* as primitive, but it seems legitimate to interpret its microsporangiate column as a fused whorl, analogous to the column of *Ephedra*.

40. 0 = strobili on undifferentiated axes, or female shoots only aggregated into compound strobili; 1 = compound male and female strobili.

This character is comparable to Hill and Crane 44 and Crane 9.14, except that Crane's (1985a) definition refers to the ovulate structures, making the character a link between conifers and cordaites. Our definition differs in requiring that both male and female strobili be aggregated, as in cordaites and Gnetales but not most conifers, even the earliest and most primitive of which (Late Carboniferous Lebachiaceae) had compound female strobili but simple male strobili at the tips of undifferentiated branches. Although the units making up the compound female strobili of cordaites and conifers are comparable and presumably homologous (axillary fertile shoots bearing spirally arranged cataphylls and sporophylls: Florin, 1951), several considerations suggest that aggregation of the units into compound strobili followed separate pathways in the two groups. The concept that conifers have primitively simple male strobili does not rule out homology between the compound female strobili of the two groups, since it is possible that the female shoots were aggregated first and then the male shoots, so that the conifer condition existed in the ancestry of cordaites. However, this seems unlikely in view of the fact that the male and female strobili of cordaites are constructed on exactly the same plan, suggesting that they were aggregated simultaneously. Furthermore, the arrangement of the fertile shoots in the female strobili is different

in the two groups: spiral in conifers, four-ranked on a bilateral axis in cordaites. Possible support for the idea that conifers were separately derived from forms without compound female strobili is provided by the Permian genus *Buriadia* (not included in our analysis), which was conifer-like vegetatively but had stalked ovules scattered on undifferentiated leafy branches (Pant & Nautiyal, 1967).

The above argument assumes that solitary male cones are primitive in conifers. Some species of *Podocarpus* have male cones aggregated into compound strobili, and Wilde (1944) considered this directly homologous with the cordaite condition, but we interpret it as an advance within conifers. This conclusion does not necessarily follow from the fact that Podocarpaceae share apomorphies with conifers over cordaites (Appendix I), since *Podocarpus* could conceivably be the basal clade in conifers. However, this is unlikely, not only because the lebachiaceous condition is seen in the oldest known conifers, but also because podocarps seem nested within conifers on such characters as siphonogamy (presumably absent in Lebachiaceae: see character 58) and presence of one ovule per cone scale.

Hill and Crane's (1982) scoring of angiosperms as having compound strobili is questionable, since comparable conditions (e.g., in Amentiferae) are usually considered derived.

PRESENCE AND SYMMETRY OF SEEDS

41, 42. 00 = no seeds; 10 = radiospermic seeds (integument with more than two evenly spaced vascular bundles); X1 = platyspermic seeds (integument strongly flattened, with two bundles in at least its lower part, or with strongly bilateral cuticle).

Our rationale for coding this character is given in the text. Hill and Crane 19 (seeds) and Crane 9.4 (integument) are essentially equivalent to 10 plus X1, but when coded separately from seed symmetry (Hill and Crane 39, Crane 9.10) they have the effect of biasing against two origins of the seed (see text).

Following Meyen (1984) and Crane (1985a), we score *Peltaspermum* as platyspermic, because the micropylar beak has two lobes and the cuticle of the integument splits into two halves (Harris, 1932a). Corystosperm seeds are usually preserved with the bent micropyle facing to the side, suggesting that they were bilateral; also, the epidermal cell arrangement is longitudinal on the margins of the seed and irregular on the faces (Thomas, 1933). Martens (1971) and Takaso (1985) described the inner integument of *Ephedra* as lacking vasculature, but Eames (1952) cited reports of two vascular strands extending varying distances up the seed in two species. Crane (1985a) scored *Welwitschia* as radiospermic, since the nucellus and integument (which has no vasculature) are circular at initiation, but because there are two bundles that extend to the base of the integument and the opening of the micropyle is transverse (Martens, 1971), we score it as platyspermic. We agree with Crane in scoring *Gnetum* as radiospermic, since its inner integument is supplied by a circle of bundles up to the point where it becomes free of the nucellus (Martens, 1971).

In our previous paper (Doyle & Donoghue, 1986), we scored Bennettitales and angiosperms as radiospermic, but here we have rescored them XX. It should be stressed that in angiosperms the "ovule" whose symmetry must be determined is not the whole anatropous bitegmic ovule (which we code as corresponding to a uniovulate cupule), but rather the nucellus plus inner integument; in Bennettitales, it corresponds to the ovule as usually defined, inside a cupule where present. The ovules in both groups are generally round in cross section, but they are highly reduced and generally lack integumentary vasculature, so that the most important indicators of symmetry are lacking. Crane (1985a) scored Bennettitales as platyspermic, based on his observation that the Triassic forms *Vardekloeftia* and *Bennetticarpus wettsteinii* have flattened seeds; however, we feel that more evidence is needed before the basic condition in the group can be determined. He scored angiosperms as radiospermic, and this view is shared by Meyen (1984), based on the presence of bundles

in a ring in the inner integument of some Euphorbiaceae; however, this family is too advanced to be directly relevant. Scoring both groups XX implies that they could have no seeds, but they are so well nested within seed plants on other characters that this is not a serious problem.

SEED ANATOMY

43, 44. 00 = megasporangium with unmodified apex; 10 = lagenostome with central column; 11, X1 = pollen chamber without central column.

In Doyle and Donoghue (1986), we considered this a binary character, with absence of a lagenostome 0 (based on its absence in progymnosperms) and its presence 1. In the resulting cladogram, it was equally parsimonious to interpret the lack of a lagenostome in higher seed ferns and coniferopsids as a retained ancestral trait or as a reversal. However, considering the ubiquity of the lagenostome in Early Carboniferous seeds (including the platyspermic genus *Lyrasperma*), it seems safe to assume that its presence is primitive in seed ferns, and that its absence in later forms is a further modification that is best coded 11. The fact that the megasporangium of higher gymnosperms differs from that of progymnosperms in having a pollen chamber also argues against coding the two groups the same. Rothwell (pers. comm.) considers the "nucellar beak" that contains the pollen chamber of medullosans, cordaites, and *Callistophyton* fully comparable to a lagenostome, and Taylor (1981) describes one medullosan seed with an apparent vestigial column; however, all these forms are more advanced in reduction of the central column. Together, these observations support coding the two structures as members of a transformation series.

Coniferopsids lack a lagenostome, but scoring them 11 would bias against the hypothesis that their seed originated independently, in which case they may never have had a lagenostome. Hence we have scored them X1, which is only one step from the progymnosperm condition, corresponding to origin of a pollen chamber. To allow wide latitude as to whether other groups are related to seed ferns or to coniferopsids, we have scored only forms with pinnately compound leaves 11 and all others X1. The absence of a pollen chamber in angiosperms is probably due to reduction, but rather than assume this, we have scored them XX.

45. Micropylar tube (Hill and Crane 49).

We previously scored progymnosperms X, meaning "not applicable," but we have rescored them 0, since they certainly do not have the advanced state. *Peltaspermum* and corystosperms have a protruding micropyle, but it is curved rather than erect; we have scored them X to allow for the possibility that this condition is homologous with that in Bennettitales and/or Gnetales.

46. Nucellar vasculature (Crane 9.7).

The significance of this feature of medullosans, cycads, and some cordaites is controversial. Walton (1953) and Meyen (1984) have regarded it as evidence that the "integument" of these groups corresponds to the cupule of lyginopterids, not the original integument, which they postulate became intimately fused to the nucellus, leaving the nucellar vasculature as a vestige. This would explain why the integument is free to the base of the nucellus in medullosans but fused most of the way in lyginopterids, although otherwise medullosans are more advanced. If other non-cupulate seeds were derived in the same way, their lack of nucellar vasculature must be due to further reduction; cordaites and *Callistophyton* have a pad of vascular tissue at the base of the nucellus (Rothwell, 1981) that might represent a vestige. These ideas were rejected by Crane (1985a), based on the similar histological zo-

nation of the integument in lyginopterids, medullosans, and other groups. The alternative is that nucellar vasculature originated de novo, perhaps associated with large seed size (a feature of medullosans and cycads). Under either interpretation, it represents an advance over the primitive seed fern condition.

Crane (1985a) scored cordaites as lacking nucellar vasculature (cf. also Stewart, 1983; Taylor, 1981), but it is reported in *Nucellangium*, which was associated with cordaites by Stidd and Cosentino (1976). In our previous paper, following Meyen (1984), we therefore scored cordaites as 1; however, because evidence on polarity within cordaites is poor, we have rescored them X.

Crane (1985a) assumed that nucellar vasculature was lacking in Mesozoic seed ferns, where such details would not be preserved. Our procedure was to score groups in which petrified seeds are not known as X, except *Caytonia*, which we scored 0 because it was studied in such detail by Harris (1958) that remnants of tracheids would probably have been seen if they existed.

Stewart (1983) says that *Williamsonia* (Bennettitales) may have vascular tissue in the nucellus, but none in the integument. This is apparently based on Sharma (1970), who described the nucellus as borne on a "central cylinder" inside a "tubular covering" (identified as the integument by Sahni, 1932) and stated that vasculature passes up a little way into the nucellus. However, Sharma also noted that the "tubular covering" thins and disappears halfway up the body of the seed, just above the level where he first recognizes a "true integument." This suggests the possibility that the "tubular covering" is actually a cupule, as described by Harris (1932b) in Triassic Bennettitales, while the "nucellus" is the basal part of the ovule, where the integument and nucellus are fused. Whether or not this is correct, the vasculature is not comparable to the well-developed system in medullosans and cycads, so we have scored Bennettitales 0.

Contrary to Crane (1985a), tracheids are reported in the nucellus of a few angiosperms (Maheshwari, 1950), but since they do not form a well-defined envelope and there is no evidence that they are basic in the group, we agree with him in scoring angiosperms 0.

47. 0 = nucellar cuticle thin; 1 = thick, maceration-resistant (Hill and Crane 22).

Our data are mostly from Harris (1954) and Hill and Crane (1982). As noted by Hill and Crane, probable dispersed glossopterid seeds described by Pant and Nautiyal (1960) have relatively thick nucellar cuticles, and Pant and Nautiyal (1984) noted the same character in seeds attached to *Ottokaria*. The nucellus in Gnetales does not appear to have an especially thick cuticle (Martens, 1971).

In our previous study (Doyle & Donoghue, 1986), we scored Bennettitales 0, based on the fact that the nucellar cuticle is thin in *Vardekloeftia*, which appears to be primitive in presence of a cupule, and which Harris (1954) assumed was also primitive in its cutinization pattern. However, in most Bennettitales the integument is free from the nucellus to its base, whereas in *Vardekloeftia* the two are fused most of the way, a presumed advance. This suggests the possibility that the thin nucellar cuticle in *Vardekloeftia* is instead secondarily reduced as a functional consequence of adnation of the integument. For this reason, we have rescored Bennettitales as X.

POLLEN/SPORE MORPHOLOGY

48. Heterospory (Hill and Crane 18).

49, 50. 00 = tetrad scar, no sulcus/pollen tube; 10 = sulcus/pollen tube; 11 = pollen tube but no sulcus (10 plus 11 are equivalent to Hill and Crane 32, pollen tube, and Crane 9.15, distal aperture).

This combines three closely correlated traits: presence or absence of a tetrad scar, a distal germination sulcus, and a pollen tube. Based on outgroup comparison, trilete microspores (prepollen), as in many Carboniferous gymnosperms, are primitive in seed plants. Pollen tubes are almost never preserved in fossils, but as far as is known origin of a pollen tube coincided with origin of a sulcus. For example, Rothwell (1972) reported a tube in *Callistophyton*, one of the oldest forms with a sulcus. However, it is conceivable that the pollen tube originated first and a definite sulcus second, to facilitate tube emergence; from a functional point of view, this might make the multiple origin of the sulcus inferred from our analysis more understandable. The aperture and tube characters are dissociated in the inaperturate pollen of *Ephedra*, *Gnetum*, and some conifers and angiosperms, all of which have a tube; since there is no doubt this condition is due to secondary loss of the sulcus, it can be coded 11. Crane scored *Ephedra* and *Gnetum* as having the derived state, on the assumption that Gnetales originally had a sulcus; our coding makes the same assumption but conveys more information.

We have not specified that a tetrad scar must be absent in state 10, since there are fossils with both a tetrad scar and a sulcus (e.g., some conifers and cordaites). This mixed condition does not merit special coding, since it is not basic to any groups considered: there are cordaites and lebachiaceous conifers with a tetrad scar and no sulcus (*Gothania*, *Potoniesporites*: Mapes & Rothwell, 1984; Millay & Taylor, 1976). Furthermore, the mixed condition is relatively rare (most cordaites and conifers have only a sulcus), suggesting a strong tendency for loss of the tetrad scar once a sulcus is present. Coding tetrad scar and sulcus characters separately would hence weight excessively two functionally correlated changes, with no increase in phylogenetic information at the level being considered.

Many medullosans have two distal grooves that have been compared with a sulcus and interpreted as a possible germination site (Taylor, 1973). However, they also have a well-developed monolete (-dilete) tetrad scar, and Millay et al. (1978) argued that germination was proximal. In any case, since some medullosans have a tetrad scar but no grooves (*Monoletes* grains extracted from *Dolerotheca*, *Parasporites*: Millay & Taylor, 1976), we assume that the grooves arose within the group.

51. 0 = pollen radially symmetrical or mixed; 1 = strictly bilateral.

This corresponds to the shift from trilete to monolete and/or sulcate conditions. *Heterangium* produced both trilete and monolete grains (Jennings, 1976); this mixed condition seems best treated as a variant of the ancestral state. Some medullosans have trilete prepollen (*Potoniea* = *Sutcliffia*?), but these were excluded for reasons discussed in **Appendix I**.

52. 0 = pollen non-saccate or subsaccate (with separation of exine layers but not clearly delimited sacs); 1 = saccate (Crane 9.9).

This formulation excludes subsaccate aneurophytes from the saccate category, where they were referred by Crane (1985a); the subsaccate condition may be ancestral in lignophytes. Some medullosans are saccate (*Parasporites*: Millay & Taylor, 1976), but the sacs are smaller and less coarsely alveolar than in other groups; we agree with Crane (1985a) in assuming that they were derived within medullosans.

53. 0 = infratectal structure alveolar (including spongy); 1 = granular or columellar (Crane 9.21).

Doyle et al. (1975) and Crane (1985a) interpreted the exine structure of *Archaeopteris* as granular, based on Pettitt (1966), but re-examination of Pettitt's figures suggests that it is actually finely alveolar, as in medullosans. Crane also scored *Lyginopteris* as granular, based

on the fact that pollen of *Crossotheca* figured by Millay et al. (1978) shows a nearly homogeneous exine. Compared with progymnosperms, which have two loose wall layers, this condition does seem to be an advance; however, it seems premature to equate it with granular, so we code it X. This is supported by the report by Stidd et al. (1985) of alveolar trilete prepollen in an isolated "lyginopterid" pollen organ. Taylor et al. (1984) described the saccate pollen of corystosperms as granular, and this was accepted by Crane (1985a); however, the sacs look alveolar under light microscopy, and the TEM figures suggest that the irregular appearance of the exine could be a result of compression of the grains and collapse of the alveolae; hence we score corystosperms X. Studies of magnoliids suggest that the columellar structure of most angiosperms is derived from granular, although there appear to be reversals in some groups (Doyle et al., 1975; Le Thomas, 1980–81; Walker, 1976); hence we have treated granular and columellar together.

54. Pollen striate (Hill and Crane 48, Crane 9.31).

Crane (1985a) differs in scoring glossopterids (with striate bisaccate pollen) as lacking this feature, which agrees with the fact that the striations run perpendicular to the sulcus in striate bisaccates but parallel to it in *Welwitschia* (and Cretaceous ephedroids), but we prefer not to exclude a priori the possibility that striations are homologous in the two groups. Striate bisaccate pollen also occurs in some conifers, but outgroup comparison with cordaites and the fact that it is restricted to more specialized members of the "Voltziales" suggest that it arose within the group. It also occurs in some peltasperms, in the broad sense of Meyen (1984).

MEGASPORES

55. 0 = megaspore tetrad tetrahedral; 1 = linear (Crane 9.6).

In our previous paper we scored *Aneurophyton* X because it is homosporous, but since there is no question that megaspores are homologous with spores in homosporous groups, and these are arranged tetrahedrally in *Aneurophyton*, we have rescored it 0. Scoring of the two lyginopterid groups is based on reports of abortive megaspores in *Stamnostoma* (Long, 1975), several other Early Carboniferous seeds (Pettitt, 1969), and *Conostoma* (Schabilion & Brotzman, 1979). Hoskins and Cross (1946) reported tetrahedral tetrads in medullosans, but this was questioned by Taylor (1965), partly on the lack of other reports at the time, and partly on the reported presence of several "megaspore tetrads" per megagametophyte. With the data on *Conostoma*, the former is no longer an obstacle, but the latter does seem anomalous; thus we have scored *Medullosa* X. Crane (1985a) scored fossil gymnosperm groups where tetrad form is unknown as linear, because of lack of a tetrad scar on megaspores examined; this extrapolation may be correct, but it seems safer to score them X. Having tetrasporic megagametophyte development, *Welwitschia* and *Gnetum* have no defined megaspores, so they are scored X.

56. 0 = megaspore wall thick; 1 = thin or lacking sporopollenin (Hill and Crane 23 plus 24, Crane 9.20).

Data are largely from Harris (1954, 1962) and Crane (1985a). Like Crane, we have combined thin and nonexistent walls; angiosperms are the only living group known to lack a megaspore wall, and it is difficult to tell whether the reported lack of a megaspore wall in fossils is real or an artifact of preservation or preparation.

A thick-walled megaspore occurs in probable dispersed and in situ glossopterid seeds (Pant & Nautiyal, 1960, 1984). Corystosperms are scored 1 on the fact (noted by Harris, 1954) that Thomas (1933) saw no megaspore in macerated seeds. Both conditions occur in

conifers; we agree with arguments of Crane (1985a) that thick walls are basic. According to Martens (1971), all three genera of Gnetales have a thin (1–2 µm) megaspore wall. He notes that the megaspore wall of *Gnetum* and *Welwitschia* is not strictly comparable with that of other seed plants, since they are tetrasporic (so the "megaspore" wall corresponds to the wall of the megaspore mother cell); however, we assume that the exine-producing machinery is homologous with that in monosporic groups.

MICROGAMETOPHYTE

57. 0 = microgametophyte with prothallial(s) and sterile cell; 1 = with only one nucleus in addition to tube and sperm nuclei.

See text for discussion.

Bennettitales (*Cycadeoidea*) have been said to have several prothallials, but Taylor (1973) argued that these were probably artifacts of folding of the exine. Similarly, reports of a multicellular antheridial jacket in cordaites are probably based on folds in the inner exine layer. However, there is a row of several cells in the center of the grain, some of which are presumably prothallials (Millay & Eggert, 1974).

58. 0 = motile sperm; 1 = siphonogamy, nonmotile sperm (Hill and Crane 17 plus 33, Crane 9.18).

Siphonogamy and nonmotile sperm appear to be strictly correlated. Since siphonogamy depends on presence of a pollen tube, and since origin of a pollen tube seems to coincide with origin of a sulcus, we have scored groups 0 if they have a tetrad scar and no sulcus, X if they have a sulcus but there is no other information on fertilization. This seems more prudent than Crane's (1985a) assumption that all fossil groups other than *Callistophyton* had motile sperm.

Rothwell (1981) compared the elongate tube of *Callistophyton* with that of conifers and suggested that it may therefore have been siphonogamous, but because studies by W. E. Friedman (pers. comm.) indicate that *Ginkgo* male gametophytes have a similar morphology early in their ontogeny, we have scored *Callistophyton* as X. We previously scored conifers 1, based on the living members; however, because the lack of a sulcus in Pennsylvanian conifers (Mapes & Rothwell, 1984) suggests that siphonogamy arose within the group, we have rescored them 0.

MEGAGAMETOPHYTE

59. 0 = megagametophyte monosporic; 1 = tetrasporic.

We assume that the tetrasporic condition in some angiosperms is derived within the group, based on the almost universal monosporic condition in primitive families (except Piperaceae). We do not follow Crane (1985a) in scoring all fossil groups 0, but we do take presence of abortive megaspores as evidence of a monosporic condition.

60. Apex of megagametophyte free-nuclear or with multinucleate cells; wall formation irregular, resulting in polyploid cells at maturity; egg a free nucleus (partly comparable to Hill and Crane 25 and 26 and Crane 9.29, no archegonia, and Hill and Crane 28, relatively free-nuclear megagametophyte).

This expresses several correlated differences between *Welwitschia* plus *Gnetum* and other groups, including angiosperms. Hill and Crane (1982) treat lack of archegonia and a partly free-nuclear megagametophyte as common features of angiosperms, *Welwitschia*, and *Gnetum*, but closer examination of ontogeny casts doubt on the comparability of the angiosperm

and gnetalian conditions and suggests that they were derived from the general seed plant condition in different ways. This view is accepted by Crane (1985a). In angiosperms, cell formation in the megagametophyte occurs at both ends, leaving only the middle of the embryo sac free-nuclear, and the egg is a well-defined cell flanked by two (rarely one) synergids. This suggests that loss of archegonia could have occurred before, during, or after origin of a free-nuclear central area. In *Welwitschia* and *Gnetum*, cell wall formation proceeds from the base toward the apex and is irregular (vs. alveolar in *Ephedra* and other gymnosperms), resulting in many multinucleate cells. In *Welwitschia*, the apex itself becomes partitioned into multinucleate cells (which produce the peculiar prothallial tubes), but in *Gnetum* the apex remains free-nuclear. In both genera, nuclei in the lower part of the gametophyte fuse by maturity, resulting in uninucleate but polyploid cells (Maheshwari & Singh, 1967; Martens, 1971). In both, free nuclei function as eggs. We assume that the condition in *Welwitschia* is related to that in *Gnetum* but less advanced. Hence it is possible that loss of archegonia in these two genera was a side-effect of a single change at the developmental level, truncation of cellularization, with no prior reduction of archegonia.

The gnetalian condition is not a logical step on the way to the angiosperm one; when compared with other seed plants, angiosperms are actually more primitive than *Welwitschia* and *Gnetum* in having normal cell formation and an egg cell. The angiosperm embryo sac is certainly highly advanced in having so few nuclei, but this says nothing about its relative status in other respects. Since there is also no evidence that the steps leading to the angiosperm condition occurred in the origin of Gnetales, angiosperms are best scored as 0 and their advances treated as autapomorphies. Scoring angiosperms 0 and *Welwitschia* and *Gnetum* 1 is appropriate in requiring at least one reversal if angiosperms are derived from ancestors with the gnetalian condition (namely, secondary cellularity of the egg).

In our previous paper we scored Bennettitales as unknown, but Sharma (1974) described *Williamsonia* as showing the normal pattern of cellularization from the micropylar end; hence we have rescored them 0.

EMBRYO

61. 0 = early embryogenesis free-nuclear; 1 = entirely cellular (Hill and Crane 38, Crane 9.2).

Hill and Crane (1982) and Crane (1985a) code this character with the opposite polarity, based on the valid observation that the free-nuclear condition of most gymnosperms is derived relative to lower vascular plants. However, the fact that cellular embryogenesis occurs only in advanced groups (*Sequoia*, which is well nested within conifers, *Welwitschia*, *Gnetum*, and angiosperms) implies that the free-nuclear condition is basic in seed plants, as recognized by Crane (1985a). Since presence of a free-nuclear stage may be functionally correlated with large size of the egg cell, the fact that Paleozoic seed ferns and cordaites had large eggs also suggests that free-nuclear is ancestral. Crane assumes that progymnosperms and fossil gymnosperm groups were cellular and free-nuclear, respectively, but because direct evidence is lacking it seems preferable to score them X.

We interpret *Ephedra* as having a free-nuclear stage, leading to precocious polyembryony. Free-nuclear embryogeny does occur in one angiosperm group, *Paeonia*; Stebbins (1974) interprets this as a retention of the gymnosperm condition, but since *Paeonia* seems well nested within higher dicots we assume it is a reversal.

62. Embryo with feeder (Hill and Crane 50, Crane 9.30).

Previously we scored Bennettitales 0, since a feeder is not described in well-preserved embryos of *Cycadeoidea*. However, because a feeder would not be expected to occur at the stage preserved, we now score them X.

Appendix III: Rejected Characters

Here we list characters that we considered using (or used in preliminary analyses) but rejected for the reasons given, including many characters of Hill and Crane (1982) and Crane (1985a). Some are autapomorphies that help support the monophyly of groups used (Appendix I); others may prove useful with better information and deserve further study.

BRANCHING

Higher order branching distichous. This feature occurs in *Archaeopteris* and early conifers, but *Svalbardia*, here included in *Archaeopteris*, has helical branching, suggesting that the distichous condition arose within archaeopterids. It could still be homologous if coniferopsids are more closely related to *Archaeopteris* than to *Svalbardia* and conifers are basal in coniferopsids, but this seems unlikely (see text). Presence of leaves on penultimate order axes (character 3) expresses much of the vegetative similarity between coniferopsids and *Archaeopteris* in a less problematical manner.

LEAF ARCHITECTURE

Multistranded midrib (in simple, pinnately veined leaves). In *Glossopteris* (and especially *Gangamopteris*) the midrib is anatomically a concentration of laminar veins (Gould & Delevoryas, 1977), and in leaf development of *Gnetum* several parallel veins differentiate in the primordium before giving off secondaries (Rodin, 1967), while in angiosperms the midrib is described as simple from its inception (Pray, 1955). It might be speculated that leaves with a multistranded midrib are closer to sphenophylls, whereas leaves with a simple midrib are closer to pteridophylls. However, the distinction between the two conditions and the basic condition within groups are both unclear. Cycads and *Pentoxylon* have multistranded midribs, and do so putatively primitive Early Cretaceous angiosperms and many extant magnoliids (Doyle & Hickey, 1976), and their mode of development is unknown.

Needle-like leaves (Crane 9.12), Cordaites foliage (Crane 9.16). As used by Crane, these are autapomorphies of conifers and cordaites, respectively. As discussed in the text, it is conceivable that they are homologous with other coniferopsid and/or gnetalian leaf types, but it is difficult to define characters so as to allow for these possibilities.

Decurrent leaf bases. Beck (1971) noted this as a similarity of *Archaeopteris* and coniferopsids, as opposed to aneurophytes, but it is difficult to score taxa in an informative manner without biasing against the Rothwell hypothesis. Under that hypothesis, conifer leaves are homologous with cataphylls; since cataphylls also have decurrent bases, all groups but aneurophytes would have to be scored 1.

One-veined leaves or cataphylls. Rothwell (1982) mentions this feature as support for relationships of *Callistophyton, Lyginopteris*, cordaites, and conifers, but it is probably redundant with presence of cataphylls (already incorporated into character 5–7), since possession of one vein may be ancestral. Alternatively, multiveined cataphylls might be considered a potential synapomorphy of cycads (Harris, 1964), glossopterids (Pant, 1977), *Caytonia* (Harris, 1964), Bennettitales (Harris, 1932b, 1969), *Pentoxylon* (Vishnu-Mittre, 1957), Gnetales (Martens, 1971), and angiosperms (which would agree with results of our analysis). However, shape and venation vary so much that comparability of the character is suspect.

EPIDERMAL FEATURES

Cuticle resistant to maceration with nitric acid. This was noted by Harris (1932a) as a feature of seed plants as opposed to ferns, and it may be a synapomorphy of seed plants over progymnosperms, since Beck (pers. comm.) was unable to prepare cuticle from *Archaeopteris*.

However, preservation of Beck's *Archaeopteris* material was probably unsuitable for cuticle preservation (G. R. Upchurch, pers. comm.); thus the ancestral condition is not established in any group considered.

Capitate glands. This feature is known in higher lyginopterids (*Lyginopteris, Heterangium Andrei*) and *Callistophyton*, but it is not definitely basic in either group. Scott (1923) considered *Heterangium Andrei* the most derived species of its genus; *Callistophyton poroxyloides* has capitate glands, but *C. boyssetii* has spines instead (Rothwell, 1981).

Orientation of stomata (parallel to venation, random, perpendicular). Parallel and random orientation vary and intergrade too much within groups, often apparently correlated with leaf shape and venation. The perpendicular orientation in Bennettitales is more distinctive, but it is restricted to the order.

Dia-, para-, anomomeristic stomatal develoment (Payne, 1979). These are potentially useful characters, but sufficient data are not yet available, and application to fossils would be necessarily speculative.

STEM ANATOMY

Group of apical cells (Hill and Crane 2). This feature is present in all extant seed plants, and the condition in progymnosperms and most other fossils is unknown, making it uninformative.

Secondary thickening (Hill and Crane 1). Present in all groups considered.

Leaf gaps (Hill and Crane 4). Beck et al. (1982) argue at length that leaf gaps of the fern type do not exist in seed plants; in eusteles, except in some derived groups, leaf traces split off from discrete primary stem bundles.

Tangential vs. radial departure of leaf traces. This distinguishes most seed plants, including *Lyginopteris* and cordaites, from progymnosperms and calamopityan seed ferns (Beck, 1970), but its distribution is poorly documented.

Many vascular bundles in the petiole. This character is not clearly comparable in different groups: sometimes it is a result of origin of leaf traces from several stem bundles, sometimes of splitting of one trace. Conditions are also poorly documented in critical Mesozoic groups.

Pycnoxylic anatomy (Hill and Crane 43). Assuming that progymnosperms show the basic condition, the polarity proposed by Hill and Crane is incorrect. In addition, this is not a single character but a vaguely defined syndrome; hence we have divided it into apparently non-redundant characters (multiseriate rays, scalariform pitting) and eliminated aspects that appear to be too variable (size of tracheids, pith, cortex).

Bordered pits in metaxylem (Hill and Crane 9). Although progymnosperms have some scalariform metaxylem pitting, they and most lower seed plants usually also have some circular bordered pits in the metaxylem, and this combination is probably basic in lignophytes.

1–2-seriate as well as multiseriate pits in secondary xylem (Hill and Crane 10). Probably uninformative, since wood with only multiseriate pitting occurs only in a few Carboniferous seed ferns, if at all.

1–2-seriate pitting only (Hill and Crane 11). This feature is not clearly basic in any group except *Ginkgo*, and it intergrades with the ancestral condition (e.g., corystosperms have mostly 1- and 2-seriate but rarely 3-seriate pitting: Archangelsky & Brett, 1961). The 1–2-seriate pitting of most conifers presumably originated within the group, since multiseriate

pitting occurs in Araucariaceae, which have many primitive features, and this polarity is supported by outgroup comparison with cordaites, progymnosperms, or seed ferns.

Metaxylem vessels (Hill and Crane 6). This character occurs in angiosperms only, and it is not basic in the group according to either the conventional interpretation or Young (1981).

Secondary xylem parenchyma. Too sporadic and poorly documented.

Ray tracheids. This character is too sporadic and poorly documented, and its polarity is unclear.

Simple Archaeopteris-*type secondary phloem vs. complex aneurophyte-type (Wight & Beck, 1984).* On the assumption that aneurophytes show ancestral lignophyte characters, the complex condition is suspected of being ancestral, but this is problematical, since outgroups lack secondary phloem. The *Archaeopteris* type occurs in *Heterangium, Medullosa,* and *Callistophyton,* but it is unclear how more advanced seed plants should be interpreted, since they usually have phloem fibers but in other arrangements.

Sieve tubes, companion cells derived from same initials (Hill and Crane 12, 13; Crane 9.38). An angiosperm autapomorphy. Sporne (1965) referred to sieve tubes and companion cells in *Ephedra* and *Gnetum* (though from different initials), and Martens (1971) stated that *Gnetum* has "plaques criblées" on the oblique transverse walls. However, this is apparently a result of terminological confusion: Martens characterizes the bark of *Ephedra* as typically gymnospermous, in contrast to the wood, and Esau (1969, pers. comm.) interprets sieve elements of both *Ephedra* and *Gnetum* as sieve cells.

Sieve tube plastids (Behnke, 1974). All groups where the character is known have the S-type except Pinaceae (presumably derived within conifers) and some angiosperms, with the P-type, so this character is uninformative at the level considered.

Loss of hypodermal fiber strands. Fiber strands seem to be ancestral in lignophytes, based on their occurrence in aneurophytes and most Carboniferous seed plants (except conifers: Rothwell, 1982); modern groups lack them. However, information on cortical structure is poor in Permian–Mesozoic groups, just where the character might be informative. *Archaeopteris* has sclerotic masses in the cortex, but it is not clear whether or not they form strands (Beck, 1971, pers. comm.).

FERTILE APPENDAGES

Pinnate or simple reproductive structures axillary or adaxially adnate to a leaf (Crane 4.2, 4.3). Unless the angiosperm carpel and its potential homologs were derived from such a structure (Stebbins, 1974; Retallack & Dilcher, 1981), which we do not wish to assume, this is a glossopterid autapomorphy (see discussion in the text and **Appendix I**).

Ovules adaxial vs. abaxial vs. terminal or marginal. This character is potentially very important, but its state is unknown, controversial, or variable in too many critical groups (see discussion in text). Townrow (1960) assumed that ovule position in *Peltaspermum* was abaxial, and this is supported by the fact that *P. rotula* has peltate "cupules" (assumed to be leaflets) with ovules on the lower side. According to Meyen (1984), ovules are abaxial in early conifers, *Buriadia,* and *Trichopitys,* but they are terminal in cordaites and the Pennsylvanian conifers described by Mapes and Rothwell (1984). Among cycads, ovules are marginal in *Cycas* but abaxial in one of the Permian taeniopterids described by Mamay (1976). Rothwell (1981) noted that ovules in *Callistophyton* are widely considered abaxial, but attached specimens are on pieces of leaf that are too small to determine orientation (e.g., based on protoxylem in veins), and in any case the ovules are so close to the margin

that the distinction is of dubious significance (Rothwell, pers. comm.). Glossopterids have been reconstructed as having ovules on the abaxial side of the "cupules" relative to the subtending leaf (Gould & Delevoryas, 1977; Retallack & Dilcher, 1981), but recently Pant and Nautiyal (1984) have concluded from better-preserved attached specimens that the cupules of *Ottokaria* were oriented adaxially. Harris (1940) interpreted the anatropous cupules of *Caytonia* as circinately reflexed leaflets, implying that the ovules inside were morphologically adaxial. This conclusion was based on several considerations: identification of the side of the rachis with several ridges as abaxial and the side with two ridges as adaxial, on analogy with similar topography in angiosperms; similarity of the cuticles of the two surfaces with the respective sides of the leaf petioles; and attachment of the cupules on the presumed adaxial side of the rachis, as leaflets are normally attached. This view was restated by Reymanówna (1974), but she was simply following Harris (Reymanówna, pers. comm.). In contrast, Retallack (pers. comm.) believes that ovules in *Caytonia* were abaxial. A distinction between laminar and apical-marginal ovules could be made more objectively, but this would be unacceptable from a theoretical point of view, since laminar ovules are known to be adaxial in some groups, abaxial in others. Reformulation in terms of anatropous cupules (character 33–35) poses fewer problems and expresses a more distinctive similarity.

Megasporophylls "unicupulate" (Crane 9.25). Implicit in our sporophyll and cupule characters (25–27, 33–35).

One vs. several ovules per sporophyll. This resembles the previous character, except that it contrasts not only Bennettitales and *Pentoxylon* but also Gnetales, conifers, and ginkgos with cordaites with several ovules per stalk and groups with complex sporophylls. Except for cordaites, this is redundant with one-veined megasporophylls, and its inclusion would over-weight a similarity between coniferopsids and Gnetales that may be simply a result of extreme reduction. Furthermore, this formulation conflicts with the hypothesis that coniferopsid sporophylls are homologous with progymnosperm fertile appendages, and hence with seed fern cupules rather than sporophylls.

Seeds enclosed (Hill and Crane 40). An angiosperm autapomorphy. The exception mentioned by Hill and Crane (*Reseda*) is surely a reversal, as they recognize.

Non-integumentary stigma (Hill and Crane 37a, Crane 9.32). Another angiosperm autapomorphy, and redundant with the previous one.

Sporophylls strongly differentiated from vegetative leaves. The patterns and degrees of specialization of mega- and microsporophylls are too varied to be equated (contrast *Caytonia*, corystosperms, *Cycas*), and largely redundant with changes already coded in characters 25–30.

CUPULES

One vs. several ovule(s) per radial cupule (Doyle & Donoghue, 1986). This was meant to distinguish uniovulate lyginopterids and Bennettitales from *Pitus*, but under our present interpretation of bennettitalian cupules as derived from either lyginopterid or anatropous cupules, the derived condition is not definitely present in more than one group. If the integument of medullosans, cycads, and coniferopsids is a modified cupule (Meyen, 1984; Walton, 1953), they too must have passed through a uniovulate stage, but this does not follow if the cupule was lost by reduction or other means.

ARRANGEMENT OF FERTILE STRUCTURES

Megasporophylls on axillary short shoots (Crane 9.13). This coniferopsid feature is largely implicit in the presence of axillary branching (character 1) and reduced sporophylls (25–27), and practically synonymous with strobili (see next character). Crane's (1985a) scoring

of Gnetales as lacking this character arbitrarily biases against the hypothesis that they are coniferopsid derivatives.

Mega- and microsporophylls aggregated on determinate axes, strobili, or flowers (roughly equivalent to Hill and Crane 14, strobili). The morphological comparability of this character in various groups (cycads, Bennettitales, *Pentoxylon*, coniferopsids, Gnetales, angiosperms) is highly uncertain, considering the varied nature of the component structures, and it seems almost redundant with whorling and/or reduction of the sporophylls. Hill and Crane (1982) scored cycads and *Ginkgo* as mixed for strobili, but the fact that only the microsporophylls are aggregated in *Cycas* suggests that strobili arose independently in cycads and other groups, and either Florin's (1949) interpretation of *Trichopitys* or the strobilar character of the axillary ovuliferous structures in the Early Cretaceous ginkgo *Karkenia* (Archangelsky, 1965) would imply that ginkgos have both male and female strobili. It is possible that Mesozoic seed ferns were tending toward aggregation, since their sporophylls are fairly differentiated from the vegetative leaves; the fact that these groups are so critical, but information on them is lacking, is another reason to omit the character.

Fertile short shoots 4-ranked on dorsiventral axis (Crane 9.17). Apparently a cordaite autapomorphy.

Sterile leaves on fertile short shoots. This similarity of *Archaeopteris*, cordaites, and conifers may be redundant with the shift of fertile appendages to last order axes (character 32).

Sterile appendages in fertile branch systems one-veined vs. several-veined. This might distinguish conifers and cordaites from *Archaeopteris*, Gnetales, and *Buriadia* (not included in the analysis), but it is too closely tied to the Beck hypothesis and the concept that Gnetales are coniferopsids. Under the Rothwell hypothesis, one-veined appendages may be ancestral in coniferopsids (cf. discussion of cataphylls).

Opposite-decussate arrangement of bracteoles in reproductive structures (Crane 9.33). In our data set (though not Crane's), this character of Gnetales would be redundant with opposite phyllotaxy.

"Unicupulate" sporophylls aggregated in heads (Crane 9.26). Use of this character of Bennettitales and *Pentoxylon* requires too many a priori assumptions on homologies and relationships: e.g., rejecting the possibility that the coniferopsid condition is equivalent, or that heads are comparable to multicarpellate receptacles of angiosperms (they differ in being "unicupulate," but this is coded elsewhere).

Perianth. This character might unite Gnetales, angiosperms, and some Bennettitales, but it is too vaguely defined (e.g., difficult to distinguish from the scale leaves on the fertile short shoots of cordaites and conifers), and the basic condition in Bennettitales is uncertain.

Strobili bisexual (Hill and Crane 15). This was an angiosperm autapomorphy in Hill and Crane's data set, but even though it occurs in two groups in the present data set (angiosperms and Bennettitales), it is still uninformative, since the basic condition in Bennettitales is uncertain. Evidence from association and stratigraphy is ambiguous: Triassic *Sturiella*, Jurassic *Williamsoniella*, and Cretaceous *Cycadeoidea* are bisexual, but Triassic–Cretaceous *Williamsonia* and Triassic *Vardekloeftia* (which is primitive in several respects) are unisexual. The abortive terminal ovule in the male flower of *Welwitschia* suggests that bisexuality once occurred in Gnetales, but this is too speculative to be used as a basis for scoring.

SEED STRUCTURE

One integument (Hill and Crane 21). This condition is derived in angiosperms but ancestral in seed plants as a whole, based on early seed ferns, conifers, and cordaites. We rejected use of this character with the opposite polarity because of developmental and positional evidence

against homology of the second integument of Gnetales and angiosperms and problems in deciding whether cupules of seed fern groups, Bennettitales, and *Pentoxylon* should be equated with extra integuments (see character 33–35).

Integument (Crane 9.4). Implicit in the presence of seeds.

Distinct micropyle (Crane 9.5). This is apparently redundant with the seed in Crane's data set and would be in ours, although the existence of isolated seeds such as *Genomosperma* with a lobed integument indicates that the two advances actually arose in sequence.

Integument fused more than half way to nucellus (Hill and Crane 20). This character is uninformative as scored by Hill and Crane, since the ancestral state occurs only in some conifers and some angiosperms. It is also highly variable and gradational (many degrees of fusion exist, and critical taxa such as Gnetales show intermediate conditions) and difficult to define because of problems of homology and polarity. In particular, if the free integument of *Medullosa*, cycads, and platyspermic groups is a modified lyginopterid cupule (Meyen, 1984; Walton, 1953), it is presumably actually derived relative to the fused condition in most lyginopterids (e.g., both *Heterangium* and *Lyginopteris*, plus *Stamnostoma* in the multiovulate group).

Integumentary "stigma" (Hill and Crane 37). This occurs only in a few conifers (e.g., *Pseudotsuga*) and is presumably derived within the group.

POLLEN MORPHOLOGY

Distal germination. Redundant with presence of a sulcus, except in inaperturate grains, where it is unverifiable.

Laminated endexine lacking (Hill and Crane 34, Crane 9.37). An angiosperm autapomorphy.

Columellae (Hill and Crane 35). Known only in angiosperms and probably derived within the group (Le Thomas, 1980–81; Walker, 1976).

EMBRYOLOGY

One functional megaspore (Crane 9.3). Redundant with presence of seeds.

Three-nuclear microgametophyte (Hill and Crane 41), microgametophyte with three or four cells (Crane 9.27), no prothallials (Hill and Crane 36). See discussion of character 57 in the text.

Megagametophyte retained on sporophyte (Hill and Crane 16). Redundant with presence of seeds, except in *Selaginella*, which is well removed from the lignophytes.

Megagametophyte with 4–16 nuclei (Hill and Crane 30, Crane 9.35). An angiosperm autapomorphy.

Micropylar end of female gametophyte relatively free-nuclear (Hill and Crane 28); archegonial initials only (Hill and Crane 25); no archegonial initials (Hill and Crane 26); archegonia lacking (Crane 9.29). These characters are partly redundant, or their correspondences in angiosperms and Gnetales are questionable on positional or developmental grounds (see discussion of character 60).

No neck canal cells (Hill and Crane 29). This character is uninformative, since it is seen in all extant seed plants and the progymnosperm condition is unknown.

Double fertilization and associated endosperm formation (Hill and Crane 31, Crane 9.36). An angiosperm autapomorphy. The second sperm nucleus has been observed to fuse with the ventral canal nucleus in *Ephedra* and with a second free egg nucleus in *Gnetum* (Martens, 1971); this may be related to double fertilization in angiosperms, but fusion with polar nuclei and resultant endosperm formation are unique.

CYTOLOGY

Polyploidy present (Hill and Crane 42). Since no groups appear to be basically polyploid, this is not a valid synapomorphy, but rather a "tendency" within groups (Hill and Crane coded conifers as derived but recognized that only a few are polyploid). However, as suggested by Ehrendorfer (1976), this tendency may be linked to the next character, which is potentially informative.

Small amount of DNA per nucleus, small chromosomes, small amounts of repetitive DNA. These features distinguish angiosperms and Gnetales from other living seed plants (Ehrendorfer, 1976), but there is no evidence on polarity from outgroup comparison. However, we note that it is most parsimonious to consider the angiosperm-gnetalian condition derived on all our cladograms.