The origins of angiosperms and their biological consequences
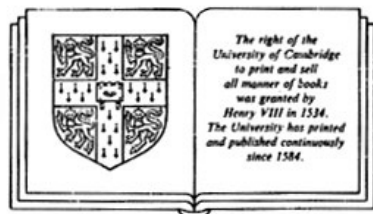
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2

The origin of angiosperms: a cladistic approach

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As the present volume illustrates, there has been renewed interest recently in the old problem of the origin and early evolution of angiosperms, stimulated in large part by studies of Cretaceous fossils. Although there is more agreement now than there was two decades ago concerning the timing and pattern of the early diversification of angiosperms, the question of their origin remains controversial, largely as a result of different ideas on how angiosperms are related to other groups of seed plants (gymnosperms). The purpose of this paper is to summarize a numerical cladistic analysis of seed plants, documented in detail elsewhere (Doyle & Donoghue, 1986b), and to explore its implications for evolutionary processes and ecological factors involved in the origin of angiosperms.

Previous ideas on angiosperm relationships

One of the first comprehensive theories concerning the relationships of angiosperms, commonly associated with the Englerian school of angiosperm systematics, was proposed by Wettstein (1907), who postulated that the angiosperms were derived from the gymnosperm order Gnetales, represented today by *Ephedra*, *Welwitschia*, and *Gnetum*. The Gnetales show more angiosperm-like features than does any other group of gymnosperms: vessels in the wood; 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; strong gametophyte reduction and cellular embryogeny in *Welwitschia* and *Gnetum*; dicotyledon-like leaves in *Gnetum* (cf. Martens, 1971). Wettstein homologized the compound strobili of Gnetales with the inflorescences of the wind-pollinated Amentiferae,

and 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 within the group.

A competing view was proposed by Arber & Parkin (1907, 1908), stimulated by recognition that some members of the Mesozoic gymnosperm order Bennettitales had flower-like bisexual reproductive structures, with a perianth, pinnate microsporophylls, and a central ovuliferous receptacle. They homologized these structures with the flowers of *Magnolia* and argued that the flowers of the Amentiferae were secondarily reduced and aggregated during reversion to wind pollination. Seeds of Bennettitales were borne singly on simple stalks, interspersed with interseminal scales, rather than on structures resembling an angiosperm carpel, and the microsporophylls were whorled and usually fused basally. Therefore, rather than deriving angiosperms directly from Bennettitales, Arber & Parkin proposed that the two groups evolved from a hypothetical common ancestor with a 'pro-anthostrobilus' bearing pinnate microsporophylls and megasporophylls. In Bennettitales, the megasporophylls were presumably reduced, but in angiosperms the microsporophylls were. Like Wettstein, Arber & Parkin assumed that Gnetales were related to angiosperms, but they interpreted the flowers of Gnetales as reduced, like the flowers of Amentiferae, citing as support the presence of an abortive ovule in the staminate flowers of *Welwitschia*.

Both of these views have subsequently fallen into wide disfavor. Relationships between angiosperms and Gnetales, assumed by both theories, have come under special criticism. First, closer examination suggests that many of their common features arose independently. For example, some presumably primitive angiosperms, such as the magnoliid dicotyledon family Winteraceae, lack vessels in the wood, suggesting derivation from ancestors without vessels rather than ancestors with them. Furthermore, vessel members in the two groups appear to be derived from different kinds of tracheid: Gnetales have vessel members with perforations that intergrade with circular-bordered pits, whereas primitive angiosperms have tracheids with scalariform pitting or vessel members with scalariform perforations (Thompson, 1918; Bailey, 1944). In general, recognition of apparently primitive features in magnoliids (vesselless wood, gymnosperm-like monosulcate pollen, leaf-like carpels and stamens) and derived features in Amentiferae (advanced vessels, triporate pollen) has cast doubt on Wettstein's arguments that are based on similarities between Gnetales and Amentiferae. Most recently, these ideas on evolution within the angiosperms have been strengthened by palaeobotanical studies. The first recognizable Cretaceous angiosperm pollen is monosulcate, whereas pollen of the amentiferous type appears much later, after a long series of intermediates, and the leaf record reveals consistent trends (Doyle, 1969, 1978; Muller, 1970; Doyle & Hickey, 1976; Crane, this volume, Chapter 5).

In addition, several lines of evidence have led to the idea that the Gnetales are related to the coniferopsid gymnosperms (conifers, Palaeozoic cordaites, and ginkgos), characterized by linear-dichotomous leaves, pycnoxylic wood, and bilaterally symmetrical (platyspermic) seeds, whereas angiosperms are related to the cycadopsid gymnosperms (cycads, Bennettitales, and so-called seed ferns), characterized by pinnate leaves, manoxylic wood, and radially symmetrical (radiospermic) seeds. For example, Gnetales have circular-bordered pits in the metaxylem and even the protoxylem, like conifers and *Ginkgo*, whereas angiosperms and cycadopsids have scalariform metaxylem pitting (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 shoot. Although Eames rejected relationships between *Ephedra* and *Welwitschia* and *Gnetum*, others have noted that all three genera have similar wood anatomy and their reproductive structures can be interpreted as modifications of the same 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.

It should be noted that the views just summarized are not universally accepted. For example, Meeuse (1963, 1972 *a*, *b*, *c*) has proposed a highly modified version of Wettstein's theory, in which angiosperm reproductive structures are derived from a polyaxial 'anthocorm' system, and Gnetales and Piperales are seen as links between 'higher cycadopsids' and typical angiosperms. Young (1981) challenged the 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 & Sattler (1982) found scalariform perforations in vessel elements of *Gnetum* and suggested that angiosperms might be derived from Gnetales after all.

Reasons for the rejection of relationships between angiosperms and Bennettitales are less clear, since the two groups have similar wood anatomy, and the presence of primitive features in magnoliids supports many of Arber & Parkin's ideas on angiosperm evolution. Recent authors have tended to emphasize the morphological differences between the parts making up the flowers of the two groups, particularly the carpels of angiosperms and the isolated ovules of Bennettitales, and to regard the similarities as convergent adaptations to insect pollination. Skepticism has centered on the fact that Arber and Parkin's attempt to reconcile these differences relied so heavily on a purely hypothetical prototype. Takhtajan (1969) and Ehrendorfer (1976) have continued to argue that angiosperms share a common ancestry with Bennettitales and that Gnetales are highly modified bennettitalean derivatives, but most discussions have focused instead on seed ferns (Cronquist, 1968; Stebbins, 1974; Doyle, 1978), in which megasporophylls are less reduced.

Among seed ferns, two Mesozoic families have attracted particular attention. Caytoniaceae, a widespread Triassic–Cretaceous group, had palmately compound leaves, simple reticulate venation, and reflexed cupules borne in two rows along the rachis of a once-pinnate megasporophyll. Corystospermaceae, a Gondwana Triassic group, had fern-like leaves and bipinnate megasporophylls. Early attempts to homologize the cupules of these groups with carpels (e.g. Thomas, 1925) were unsuccessful (the cupules appear to be modified leaflets rather than whole sporophylls borne on a stem), but several authors have noted that reduction to one ovule per cupule (seen in corystosperms) would result in a structure like the anatropous, bitegmic ovule of angiosperms, with the outer integument corresponding to the cupule wall (Gaussen, 1946; Stebbins, 1974; Doyle, 1978). The carpel itself might then be derived from the sporophyll rachis by expansion and folding to enclose the ovules. Doyle (1978) pointed out that relationships with Mesozoic seed ferns would be consistent with the concept of Takhtajan (1969) that many of the conspicuous innovations of angiosperms can be interpreted in terms of paedomorphosis (phylogenetic shifting of juvenile features to later stages of ontogeny): simple leaves and stamens, scalariform secondary xylem pitting, condensation of sporophylls into flowers, closed carpels (suggesting unopened conduplicate leaves), the primordial state of ovules at fertilization, the reduced, partly free-nuclear megagametophyte, and lack of archegonia. Doyle argued that the reduced size, rapid functioning, and changes in relative proportions of angiosperm structures relative to those of seed ferns suggest an origin through

progenesis (paedomorphosis resulting from precocious reproductive maturity, as opposed to neoteny, paedomorphosis resulting from retarded somatic development: Gould, 1977). Since Gould associates progenesis with selection for high reproductive rates (*r*-selection), this hypothesis would be consistent with the idea that early angiosperms were weedy colonizing species, as proposed by Stebbins (1974) and supported by Doyle & Hickey (1976) on Cretaceous fossil evidence (cf. Crane, this volume, Chapter 5).

Also much-discussed are the predominantly Permian glossopterids of Gondwana, considered to be coniferopsids by Schopf (1976) but seed ferns by Gould & Delevoryas (1977) and most other authors. Glossopterids had simple leaves with simple reticulate venation and fructifications consisting of a leaf bearing one or more cupule-like structures on its adaxial side. Stebbins (1974) and Retallack & Dilcher (1981) argued that the ovulate structures could be transformed into an angiosperm carpel by reduction to one ovule per cupule (seen in one glossopterid, *Denkania*) and folding of the leaf.

This brief review by no means exhausts current hypotheses on angiosperm relationships. For example, several authors support a polyphyletic origin of angiosperms (e.g. Meeuse, 1963, 1972 *a, b, c*; Hughes, 1976; Krassilov, 1977), and Krassilov and Hughes have suggested that some angiosperms were derived from the Mesozoic ginkgophyte order Czekanowskiales, which had seeds enclosed in bivalved capsules.

Previous cladistic studies

Cladistic analysis offers the most rigorous method for formulating and testing hypotheses on relationships of groups, and hence for elucidating evolutionary events and processes involved in their origin. Cladistic studies attempt to reconstruct the branching pattern of phylogeny from the distribution of shared derived character states (synapomorphies), and hence to identify clades or monophyletic groups in the strict sense of Hennig (1966). The most widely accepted method for determining ancestral versus derived character states (polarity) is outgroup comparison: if one character state is restricted to the group in question but another occurs in related groups, the latter is considered to be ancestral. Most commonly, hypotheses of relationship are judged and character conflicts resulting from convergence and reversal (homoplasy) are resolved using the criterion of parsimony; that is, the scheme is preferred that requires the fewest character state changes. It should be noted that parsimony analysis does not assume that evolution follows a most

parsimonious path; it is simply a method of finding the hypothesis that is best supported by the totality of known characters (Farris, 1983).

The first detailed cladistic analysis of seed plants, which considered extant groups only, was performed by Hill & Crane (1982). They presented several almost equally parsimonious arrangements but favored one in which angiosperms are the sister group of conifers plus Gnetales, and cycads plus *Ginkgo* are the sister group of the angiosperm–conifer–gnetalean clade. This breaks up both cycadopsids and coniferopsids and calls into question the cycadopsid affinities of angiosperms. Unfortunately, Hill and Crane's study suffered from problems in character analysis (Doyle & Donoghue, 1986b): questionable polarity decisions, often because fossil groups were not considered; redundant characters (e.g. siphonogamy and non-motile sperm); vaguely defined characters (e.g. strobili); questionable scoring of groups; and omission of many potentially informative characters (most aspects of leaf architecture, organization of the ovule-bearing structures, and pollen morphology). Furthermore, over half of the 50 characters used are either invariant in seed plants or advances of terminal groups (autapomorphies) or Gnetales, and are therefore not informative in determining relationships among major groups. In addition, Hill and Crane did not take advantage of numerical cladistic (computer-assisted) methods, which are all but essential when character conflicts are common and equally or more parsimonious alternative relationships are easy to overlook.

This analysis was subsequently completely redone by Crane (1985), taking into account fossil groups, correcting most of the problems in character analysis seen in Hill & Crane (1982), and using numerical techniques. He concluded that coniferopsids were derived from platyspermic seed ferns, as proposed by Rothwell (1982), rather than from *Archaeopteris*-like progymnosperms (Meeuse, 1963; Beck, 1971, 1981), but he separated Gnetales from the coniferopsids and grouped them with angiosperms, Bennettitales, and *Pentoxylon* in a clade related to Mesozoic seed ferns, which are also platyspermic. He emphasized 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, these results reconcile Arber & Parkin's (1907, 1908) views on relationships of angiosperms, Bennettitales, and Gnetales and more recent comparisons between angiosperms and Mesozoic seed ferns. However, this analysis is still unsatisfying in several respects. Some characters were coded in ways that bias the results toward particular hypotheses (e.g. one

functional megaspore, integument, and micropyle were coded separately, and platyspermic seeds were coded as derived from radiospermic, thus favoring a single origin of the seed). Several characters were omitted that have been cited as evidence for alternative relationships (e.g. similarities in branching pattern in *Archaeopteris* and coniferopsids, anatomical similarities between Gnetales and coniferopsids). In some cases, the ancestral state was assumed to be present in fossil groups for which information is lacking (e.g. angiosperms are linked with Gnetales on one character, siphonogamy, but, as Crane recognizes, there is no reason to assume that siphonogamy did not exist in Bennettitales and *Pentoxylon*). For these reasons, it is difficult to judge how much stronger is the support for Crane's scheme than for alternatives.

In an attempt to overcome these problems, we undertook our own numerical cladistic study, which differs from previous analyses in several respects. First, we made a great effort 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 major competing morphological theories. 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 lengths of alternative trees. One preliminary analysis was described in a discussion of relationships between angiosperms and Gnetales (Doyle & Donoghue, 1986a); results of that study differ from those summarized here (Doyle & Donoghue, 1986b) largely in grouping angiosperms, Bennettitales, and Gnetales with cycads and *Medullosa* rather than with *Caytonia* and glossopterids. This change is due largely to the recoding of sporophyll characters in cycads and ovule and cupule characters in Bennettitales, *Pentoxylon*, and angiosperms, on the basis of data and arguments of Crane (1985) and recognition of subtle biases in our previous character codings.

Methods

Choice of taxa for our analysis (Table 2.1) was necessarily a compromise based on: (1) a desire to represent all major seed plant groups and to recognize only monophyletic groups, (2) the variable quantity and quality of information available on different groups, and (3) potential relevance to major problems of seed plant phylogeny. Thus we treated *Ephedra*, *Welwitschia*, and *Gnetum* as separate taxa because we hoped to

Table 2.1. *Terminal taxa used by Doyle & Donoghue (1986b), with abbreviations used in Figure 2.1*

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

test the recurrent suggestion that Gnetales are polyphyletic. In order to test the hypothesis that cycadopsids and coniferopsids are derived independently from progymnosperms (Meeuse, 1963; Beck, 1971, 1981), we included two groups of progymnosperms (*Aneurophyton, Archaeopteris*) as well as seed plants. We split up many conventional taxa, such as seed ferns, because they are thought to be paraphyletic; that is, grade taxa, some members of which are more closely related to various 'higher' groups than to each other. Other groups may also be paraphyletic but contain many members that are too incompletely known to be sorted into assuredly monophyletic taxa; in such cases, we selected one particularly well-reconstructed or phylogenetically critical member for analysis (e.g. *Aneurophyton, Peltaspermum, Medullosa*). Where the amount of information on various organs is marginal, our decision on whether or not to include groups was often based on potential relevance to angiosperm relationships: thus we included *Caytonia* and glossopterids but not two interesting Permian coniferopsid groups, *Buriadia* (Pant & Nautiyal, 1967) and Angaran 'cordaites' (Meyen, 1984).

Czekanowskiales were excluded because so many key aspects of their morphology are unknown or obscure, and because most characters that are available can be interpreted in ginkgoalean terms (Meyen, 1984).

While this procedure resulted in many small taxa, several large, diverse groups such as conifers and angiosperms were left undivided because they have so many apomorphies that they can be assumed safely to be monophyletic. When characters vary within such groups, we attempted to identify the basic conditions, which were usually clear from comparison with any of several plausible outgroups (e.g. monosulcate pollen in angiosperms), probable relationships within the group, and the stratigraphic record. Thus we used magnoliid dicotyledons and pre-Albian fossils as guides in coding angiosperms and Permo-Carboniferous Lebachiaceae in coding conifers. Since many authors have questioned whether angiosperms are monophyletic, it is worth noting that they are united by at least nine apomorphies: 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 associated with endosperm formation. There are some exceptions to these characters, but they occur in taxa that seem to be well-enough nested within angiosperm groups to assume that they represent secondary reversals or elaborations. 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.

Choice of characters involves preliminary hypotheses on homology, by which we mean any trait inherited from a common ancestor and its subsequent transformations. Potential homology may be recognized by analysis of positional and developmental relationships of structures (Kaplan, 1984), but the ultimate test of homology is congruence with the totality of evidence on phylogenetic relationships. In seed plants, several alternative derivations 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.

In numerical methods of the sort used here, 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). 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 analysis we used 62 binary characters, defined briefly in the Appendix (p. 42; for details, see Doyle & Donoghue, 1986b). Toward our goal of testing alternative hypotheses of seed plant evolution in as unbiased a way as possible, we allowed relatively wide leeway in treating similarities as potential homologies. 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 attempted to avoid bias by scoring groups X. In compiling characters, we consistently excluded autapomorphies; although these are important in determining that the groups used are monophyletic, they contribute nothing to the understanding of relationships between groups and give a false sense of the amount of information present in the matrix. We also attempted to eliminate redundant (developmentally correlated) characters, usually identified as such because they changed simultaneously on cladograms obtained in preliminary analyses and could be plausibly attributed to the same morphogenetic factors (e.g. extension of circular-bordered pitting into both the metaxylem and the protoxylem in conifers, ginkgos, and Gnetales).

Polarities were determined by outgroup analysis (Maddison, Donoghue & Maddison, 1984), which necessitated a preliminary analysis of relationships among vascular plants as a whole (Doyle & Donoghue, 1986b). We concluded that progymnosperms and seed plants form a monophyletic group, united by possession of both secondary xylem and phloem, periderm, and cortical fiber strands (lost in more advanced seed plants). Several other advances of living seed plants in organs that are not preserved in progymnosperms (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 row) could be synapomorphies of progymnosperms and seed plants or of seed plants alone. Cladoxylales, sphenopsids, and ferns are the closest outgroup(s) of progymnosperms and seed plants, trimerophytes, the next outgroup. Comparison with these groups indicates that Aneurophyton retains the ancestral state for the group in all characters considered;

hence, it can be used as a functional outgroup for assessment of polarities in the remaining taxa (the functional ingroup: Watrous & Wheeler, 1981).

On this basis, deciding on polarity and the resulting coding was often relatively easy. The greatest difficulties arose in coding multistate characters, where the ancestral state is clear but there are alternative interpretations of relationships of the derived states. A good example concerns major categories of leaf morphology. Most workers agree that the pinnately compound leaves of seed ferns were derived from branch systems bearing dichotomous leaves, as in Devonian progymnosperms (Meeuse, 1963; Beck, 1971, 1981; Rothwell, 1982; Meyen, 1984), and the once-pinnately organized leaves of cycads, Bennettitales, and angiosperms are clearly derived relative to fronds. Progymnosperms can thus be coded 000, seed ferns 100, and once-pinnate groups 110. However, there is disagreement over the homologies of the linear-dichotomous leaves of coniferopsids. On the basis of similarities in branching patterns and anatomy, Beck (1971, 1981) suggested that coniferopsids were independently derived from Archaeopteris-like progymnosperms. The leaves of coniferopsids, which are Archaeopteris-like in groups such as Ginkgo, would thus be directly homologous with those of progymnosperms, although at least one change would have to be postulated: coniferopsids with dichotomous leaves also have cataphylls (scale leaves), like other seed plants, but progymnosperms do not. More recently, however, on the basis of the discovery of coniferopsid characters such as platyspermic seeds and saccate pollen in the Late Carboniferous seed fern Callistophyton, Rothwell (1982) proposed instead that coniferopsids were derived from seed ferns, perhaps by heterochrony: suppression of the fronds and production of cataphylls throughout the life of the plant (cf. also Meyen, 1984). Coding coniferopsids 001, one step from progymnosperms, would be appropriate under the Beck hypothesis but would bias against the Rothwell hypothesis by making derivation from seed ferns take two steps, whereas coding coniferopsids 101, one step from seed ferns, would bias against the Beck hypothesis. We attempted to avoid these biases by coding coniferopsids X01, one step from either progymnosperms (where X = 0) or seed ferns (where X = 1). We coded the linear leaves of Ephedra and Welwitschia XX1 in order to allow for a still broader range of prototypes, since it has been postulated that Gnetales are related to groups coded both X01 (coniferopsids) and 110 (Bennettitales, angiosperms). Subtle biases can be introduced by this technique,

since it adds an extra step (or steps) when an X-coded state is positioned between two other states, but these are unlikely to be serious in the present case (Doyle & Donoghue, 1986 *b*).

We used similar systems to code sporophyll morphology and seed symmetry, which also show different pathways of derivation under the Beck and Rothwell hypotheses. We also used X to code autapomorphies that may be derived either directly from the ancestral state or from another derived state (e.g. the three-nucleate microgametophyte of angiosperms versus the more complex basic condition and the partially reduced condition in *Welwitschia* and *Gnetum*).

For our analyses, we used two basically similar programs: the Wagner parsimony algorithm in PHYSYS (Mickevich & Farris, 1982) and the Mixed Method Parsimony algorithm with the Wagner option in PHYLIP (Felsenstein, 1985). Both programs attempt to find the branching diagram that minimizes the total number of character state transitions, treating forward changes and reversals equally. We attempted to evaluate alternative hypotheses by adding 'dummy' synapomorphies to the matrix to force particular taxa together and then subtracting the corresponding numbers of steps after analysis, or by employing the user tree option in PHYLIP, which allows one to specify whole trees and determine their length.

Because of the large number of possible trees, 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 what taxa have already been entered. PHYSYS determines the order of entry based on an advancement index, but in PHYLIP the order of entry is specified by the user. Finding most parsimonious trees with both programs required considerable experimentation and familiarity with possible alternative relationships, much of it gained from preliminary analyses. PHYSYS improves the chances of finding most parsimonious trees by global branch-swapping, but the shortest trees that we obtained with PHYSYS (124 steps) were found by forcing together taxa using dummy characters. Some of our shortest trees (123 steps) were obtained with PHYLIP, by judicious shuffling of the order of entry (entering taxa roughly in order of advancement but placing possible 'linking' taxa in various arrangements before specialized and problematical ones) and with the user tree option; others were found by W. E. Stein (personal communication), using the PAUP program of D. L. Swofford.

Results

One of our most parsimonious cladograms is shown in Figure 2.1; others differ in reversing Bennettitales and *Pentoxylon* and/or in rearranging *Callistophyton*, coniferopsids, corystosperms, and cycads in various ways. 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 extant groups of seed plants. Seed plants are thus a monophyletic group, initially united by cataphylls and pinnately compound leaves, multiseriate rays, fused pollen sacs, radiospermic seeds with a lagenostome, and probably axillary branching (all modified or reversed in some members). *Medullosa* and higher seed plants are linked by loss (or transformation into a new integument) of the lyginopterid cupule, reduction of the lagenostome to a 'normal' pollen chamber, and bilateral pollen.

Excluding later reversals, the clade above *Medullosa* is united by normal eusteles, platyspermic seeds, saccate pollen, and linear megaspore tetrads. The representative that has retained the most primitive characters is the Late Carboniferous seed fern *Callistophyton*. Coniferopsids are either basal or nested within the clade, supporting the hypothesis that they were derived from *Callistophyton*-like platyspermic, saccate seed ferns (Rothwell, 1982) rather than *Archaeopteris*-like progymnosperms (Beck, 1971, 1981). However, trees with coniferopsids linked with *Archaeopteris* are only one step longer (124 steps), implying that the Beck hypothesis is still a viable alternative. A sulcus and pollen tube and abaxial microsporangia arise independently within coniferopsids and below *Callistophyton*. The remaining groups, which include Permian and Mesozoic seed ferns, are initially united by multilacunar nodes (a convergence with medullosans) and secondarily free microsporangia (also seen in coniferopsids). Unexpectedly, cycads are linked with the Permo-Triassic seed fern *Peltaspermum* (on secondary loss of saccate pollen), not with medullosans as is often suggested; this means that cycads are secondarily radiospermic, which is consistent with the fact that seeds of Permian taeniopterids (considered as primitive cycads by Mamay (1976)) appear to be flattened and *Cycas* seeds have bilateral symmetry (Meyen, 1984).

The angiosperms also belong in the platyspermic group, forming a clade with Bennettitales, *Pentoxylon*, and Gnetales, initially united by leaves with simply pinnate organization, scalariform pitting in the
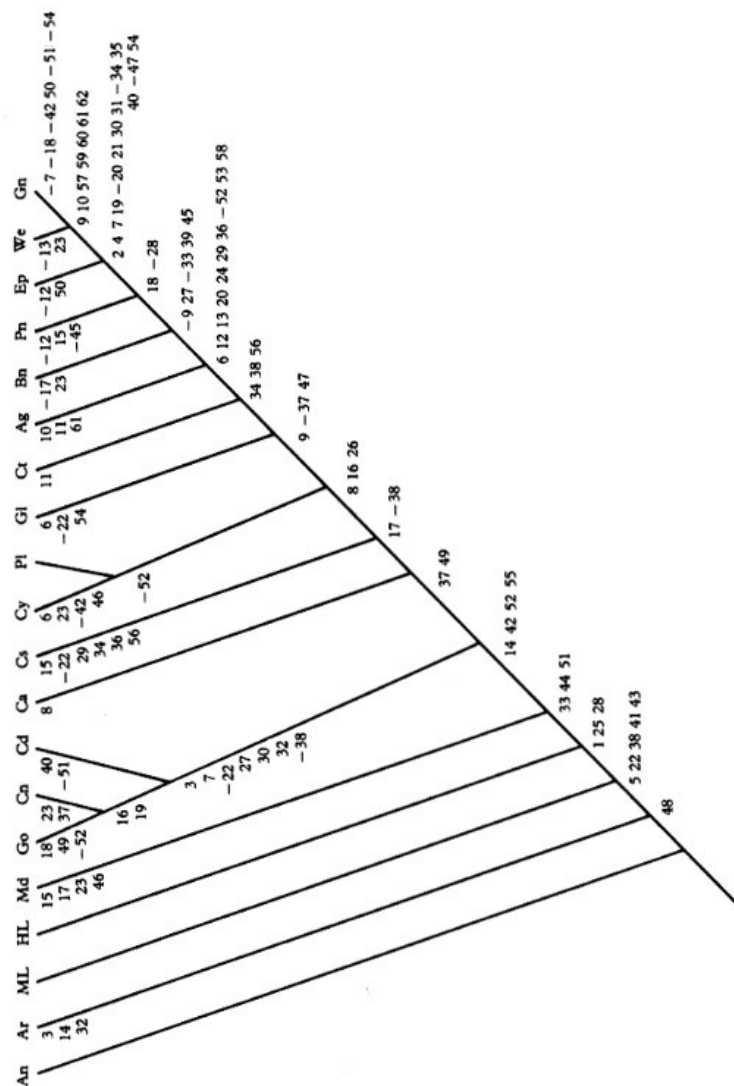
Figure 2.1. Representative most parsimonious 123-step cladogram of progymnosperms and seed plants (Doyle & Donoghue, 1986b). Taxa are defined in Table 2.1, characters in the Appendix. Minus signs before characters indicate reversals.

secondary xylem, once-pinnate microsporophylls, one ovule per cupule, secondarily non-saccate pollen, granular exine structure, and syndeto-cheilic stomata. Other possible synapomorphies are a tunica layer in the apical meristem, siphonogamy, and lignin chemistry (Mäule reaction), characters seen in angiosperms and Gnetales but not preserved in fossils. Since all four groups show strong aggregation of sporophylls into flower-like reproductive structures, we will refer to this clade as the anthophytes. 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 of the larger group to which they belong. This contrasts sharply with recent suggestions that flowers originated within the angiosperms (Meeuse, 1963, 1972a, b, c; Krassilov, 1977; Dilcher, 1979; Meyen, 1984). Recognition of the anthophyte clade is a striking agreement with Crane (1985), although our scheme differs slightly in relating anthophytes most closely to *Caytonia* and glossopterids, whereas he interpolated corystosperms between *Caytonia* and anthophytes. Glossopterids are linked with *Caytonia* and anthophytes on reticulate venation (later lost below Bennettitales), a shift away from abaxial microsporangia, and a thick nucellar cuticle; *Caytonia* is linked with anthophytes on anatropous cupules (presumably homologous with the glossopterid cupule), secondary formation of microsynangia, and reduction of the megaspore wall. The cupules of glossopterids and *Caytonia* presumably represent enrolled leaflets bearing laminar ovules, since the original lyginopterid cupule was lost several nodes below.

Within anthophytes, our results imply that angiosperms are the sister group of the remaining taxa. Bennettitales, *Pentoxylon*, and Gnetales share several advances over angiosperms: erect, solitary ovules (cupules), whorled microsporophylls, and possibly a micropylar tube (if lost in *Pentoxylon*). This scheme again differs slightly from that of Crane (1985), who groups angiosperms with Gnetales (as proposed by Arber & Parkin, 1908) and Bennettitales with *Pentoxylon*; as noted above, Crane links angiosperms and Gnetales on siphonogamy, which may be basic in anthophytes. The three genera of Gnetales are in turn united by multiple axillary buds, opposite-decussate leaves, vessels, loss of scalariform secondary xylem pitting, extension of circular-bordered pitting into the protoxylem, one-veined microsporophylls, a single terminal ovule, loss of the cupule, origin of a new outer integument from the perianth of the ovulate flower, compound strobili, reduction of the nucellar cuticle, and
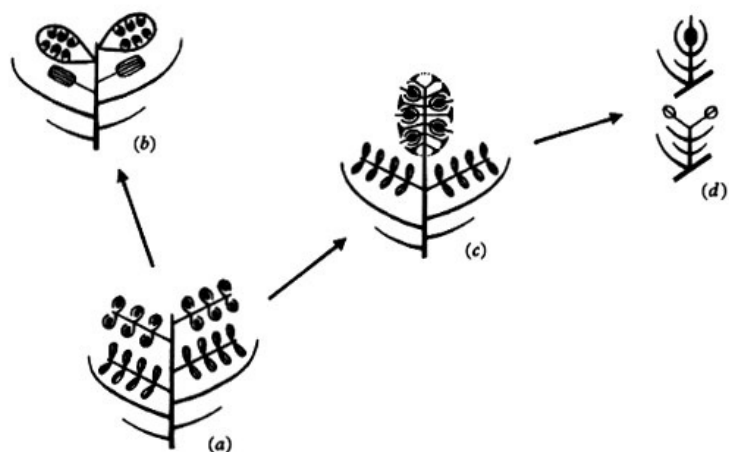
Figure 2.2. Major transformations in reproductive structures of anthophytes inferred from Figure 2.1. (*a*) Hypothetical common ancestor; (*b*) angiosperms; (*c*) Bennettitales; (*d*) Gnetales.

probably linear leaves and striate pollen (assuming reversals in *Gnetum*). Of these, linear leaves, the pitting characters, reduced microsporophylls, and compound strobili are convergences with coniferopsids. Within Gnetales, *Welwitschia* and *Gnetum* share additional advances, many of them convergences with angiosperms: vein anastomoses, interpolated higher-order veins, reduction of the male gametophyte, a tetrasporic megagametophyte with free-nuclear eggs, cellular embryogeny, and a feeder in the embryo. Although Gnetales are thus the closest living relatives of angiosperms, most of the commonly cited similarities between the two groups (vessels, dicotyledon-like leaves, simple stamens, embryology) arose independently, and most of the homologies are rather cryptic (siphonogamy, tunica–corpus, lignin chemistry, reduced megaspore wall, granular exine). As we discuss elsewhere (Doyle & Donoghue, 1986*a*), this goes far toward explaining why angiosperm–gnetalean relationships have been widely rejected (including by one of us: Doyle, 1978).

Inferences concerning floral evolution in the anthophytes are summarized in Figure 2.2. Although our results indicate that Gnetales are the closest living relatives of angiosperms, they in no way support derivation of angiosperms from Gnetales, as in Wettstein's (1907) Pseudanthial Theory. Rather, they are more consistent with the views of Arber & Parkin (1907, 1908), that angiosperms, Bennettitales, and Gnetales were

derived from a common ancestor with bisexual flowers and pinnate megasporophylls and microsporophylls, and that the flowers of Gnetales were secondarily reduced and aggregated in response to wind pollination, like the flowers of Amentiferae within angiosperms. In retaining relatively leaf-like carpels, angiosperms are primitive, but they are advanced in having simplified stamens (with two pairs of pollen sacs representing synangia of the *Caytonia* or bennettitalean type). Bennettitales are primitive in retaining pinnate microsporophylls, but megasporophylls were reduced to single ovules in the common ancestor of Bennettitales and Gnetales, and Gnetales went on to simplify the microsporophylls as well. Whether anthophyte flowers were originally bisexual is equivocal but consistent with present data (Doyle & Donoghue, 1986*b*). We find the agreements with Arber & Parkin (1907, 1908) all the more significant because our results were obtained with a large set of characters, many of which were not known to them, and without their speculative assumption that the clade had bisexual strobili originally.

Experiments

These results go far toward bridging the gap between angiosperms and other seed plants, since they allow angiosperm flowers, carpels and bitegmic ovules to be homologized with specific structures in related groups. The same is true of the wood anatomy, stomatal structure, and granular monosulcate pollen of primitive angiosperms, all of which resemble Bennettitales. However, there are several reasons for concern. Even our most parsimonious trees include a large amount of homoplasy: the presence of 123 steps with 62 binary characters means, on average, almost one convergence or reversal per character. 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, and the results may be unstable (sensitive to addition, deletion, or reinterpretation of characters). Furthermore, although our results are generally consistent with the stratigraphic record, derivation of angiosperms and Bennettitales plus Gnetales from a common ancestor indicates that the line leading to angiosperms existed at least as far back as Bennettitales (Late Triassic), but convincing angiosperm remains are not known until the Cretaceous. The loss and reappearance of reticulate venation within the anthophytes may also seem implausible. 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. In general, these experiments

indicate that several major clades are quite stable (i.e. hard to break up without adding a large number of steps), but they can be placed almost equally parsimoniously in several different positions.

Experiments relating to non-angiospermous groups are discussed in detail by Doyle & Donoghue (1986*b*); here we will concentrate on experiments that bear on angiosperm relationships. Our primary result is that the position of the anthophyte clade is somewhat unstable, but the group itself is robust, implying that its unity can be assumed with some confidence and used as a basis for further inferences. This can be seen by comparing the lengths of trees in which anthophytes as a whole, and particular subgroups alone, are moved to alternative positions. For example, moving all anthophytes into a clade with cycads and *Medullosa* (as in Doyle & Donoghue, 1986*a*) adds four steps (127), whereas associating Bennettitales and Gnetales with cycads and *Medullosa* but leaving the angiosperms linked with *Caytonia* and glossopterids adds nine steps.

The least securely included group in the anthophytes appears to be the Gnetales; only four extra steps are needed to move them into the coniferopsids (linked with ginkgos on primary xylem pitting, two-trace nodes, and non-saccate pollen). However, trees only two steps longer than our best trees are obtained when the anthophytes as a whole are moved to the same position, with Gnetales as the sister group of *Pentoxylon*, Bennetttitales, and angiosperms. This rather disconcerting result suggests that the last three groups originated from coniferopsids via Gnetales-like intermediates, as envisioned for angiosperms by Wettstein (1907); however, the fact that Bennettitales and *Pentoxylon* are interpolated between angiosperms and Gnetales would suggest that the angiosperm flower originated by elaboration rather than by aggregation of simple units into pseudanthia. Since ginkgos are the sister group of anthophytes in this scheme, it recalls the suggestion of Krassilov (1977) that angiosperms are derived from Czekanowskiales, which we interpret as ginkgophytes (cf. Meyen, 1984). We find such 'neo-englerian' trees highly implausible in morphological terms, since they require first drastic reduction and then re-elaboration of leaves and sporophylls into a pinnate pattern convergent with that of Mesozoic seed ferns and cycads, a shift from cycadopsid to coniferopsid anatomical features and back again, and an origin *de novo* of the cupule or outer integument. It is easier to imagine that the similarities between the simple appendages of Gnetales and coniferopsids are due to independent reduction. These results show that earlier authors were right in seeing

evidence for relationships between the Gnetales and coniferopsids, but the links between the Gnetales and other anthophytes are stronger.

The most parsimonious alternative positions of the anthophytes are found with different arrangements of cycads and the various platyspermic taxa. Relationships among these groups are highly unstable, undoubtedly reflecting the lack of data on many characters in Permian and Mesozoic fossils. We obtained a large number of 124-step trees with cycads interpolated between *Medullosa* and the platyspermic clade, in which case their commonly cited similarities with medullosans (multilacunar nodes, secretory canals, nucellar vasculature) could be homologies, and the ancestor of all higher groups would be more like *Medullosa* than *Callistophyton*. Most of these trees associate coniferopsids with glossopterids and/or *Peltaspermum*, which implies that the lack of a sulcus in cordaites and primitive conifers is a reversal rather than a primitive retention. Some trees link anthophytes with corystosperms alone, with *Caytonia* and corystosperms (in either order) but not glossopterids, or with all three groups in various orders (cf. Crane, 1985). Others diverge more fundamentally in linking *Caytonia* directly with angiosperms, on the basis of reticulate venation and flat guard cells; however, this is not a major challenge to the unity of the anthophyte clade, since the closest relative of the anthophytes is simply shifted inside the group. These variations have generally consistent morphological implications, since all three seed fern groups have cupules and sporophylls that can be homologized with angiosperm structures in similar ways.

Many of these uncertainties might be resolved by new data on missing characters in fossil groups. For example, the presumed homology between bitegmic angiosperm ovules and the cupules of Mesozoic seed ferns implicitly requires that both structures are derived from circinately enrolled leaflets with ovules on their *adaxial* surface. This is based not 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 (equivalent to the original unitegmic ovule), the funicle (the basal part of the leaflet), and the micropyle (its reflexed tip) relative to the whole carpel (Doyle, 1978, p. 384). We did not include adaxial versus abaxial ovule position in the data matrix because relevant information is lacking in many critical groups. Harris (1940) presented indirect evidence that the cupules of *Caytonia* are oriented adaxially, but this is questioned by G. Retallack (personal communication). One problem is that ovule position appears to be abaxial in other platyspermic groups (e.g.

Callistophyton, peltasperms; Meyen, 1984). If the cupules of glossopterids were borne facing the subtending blade, as reconstructed by Gould & Delevoryas (1977), ovule position would also be an obstacle to a close relationship between angiosperms and glossopterids. Retallack & Dilcher (1981) circumvented this problem by comparing angiosperms with the glossopterid genus *Denkania*, which had orthotropous, uniovulate cupules, and by interpreting angiosperms as being primitively orthotropous. However, this may have been unnecessary, since Pant & Nautiyal (1984) have reported that ovules in the glossopterid fructification *Ottokaria* were oriented adaxially.

A final reason for confidence in relationships among angiosperms, Bennettitales and Gnetales is that they share several features excluded from the original data set because of problems in interpretation that may, with hindsight, be additional synapomorphies. One of these, flower-like strobili, has already been discussed. Anthophytes also show several striking parallel trends; these cannot be used as synapomorphies, but they may reflect shared genetic advances (cf. Cantino, 1985). Ehrendorfer (1976) noted that Gnetales differ from other gymnosperms and resemble angiosperms in having relatively small chromosomes, less repetitive DNA, and extensive polyploidy. Gnetales also show fusion of the second sperm nucleus with one or another nucleus of the megagametophyte (Martens, 1971), a possible precursor of double fertilization of the angiosperm type. 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 be suspected in Bennettitales and *Caytonia*, on the basis of their small seed size. Anthophytes also show strong tendencies for adaptation to hot and/or dry conditions. This is clearest for angiosperms and Gnetales, which were most abundant and diverse in the Early Cretaceous tropics (Africa–South America, southern China), associated with evidence of aridity (Brenner, 1976; Doyle, Jardiné & Doerenkamp, 1982). However, it is also true for 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). There is also evidence that early angiosperms and Gnetales both tended to occupy disturbed flood-plain habitats (Doyle & Hickey, 1976; Doyle *et al.*, 1982; Upchurch & Crane, 1985; Crane, this volume, Chapter 5), 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.

Within anthophytes, the strength of different links varies considerably. It is highly unparsimonious to force angiosperms into Gnetales, as the sister group of *Welwitschia* and *Gnetum* (133 steps) or *Gnetum* alone (136 steps), as implied by suggestions that angiosperms are derived from Gnetales (e.g. Muhammad & Sattler, 1982). However, only two extra steps (125) are needed to link angiosperms directly with the Bennettitales, in which case the sister group of anthophytes is corystosperms rather than *Caytonia*. Three extra steps are required to link angiosperms with Gnetales, as proposed by Crane (1985).

General implications

Some further implications of our results for the evolution of angiosperms and related groups may be discussed with reference to Figure 2.3, which shows three phylogenetic trees and associated character changes plotted against time, with *Pentoxylon* omitted for clarity.

As already noted, our most parsimonious cladograms (Figures 2.1, 2.3(*a*)) imply that simplified leaves, syndetocheilic stomata, non-saccate granular pollen, and aggregation of sporophylls into flowers are homologies of angiosperms and other anthophytes, and that reduced megasporophylls, whorled microsporophylls, and a micropylar tube are further advances of Bennettitales and Gnetales. A problem is that this arrangement entails a gap in the record of the angiosperm line from the Late Triassic to the Early Cretaceous. The idea that angiosperms underwent much of their radiation before the Cretaceous (Axelrod, 1952, 1970) conflicts with present evidence for rapid diversification during the Cretaceous, but the earlier existence of primitive angiosperms cannot be ruled out (Doyle, 1969, 1978; Muller, 1970). Late Triassic monosulcate pollen with tectal perforations and columellae (Cornet, 1977) and Jurassic dicotyledon-like leaves (e.g. *Phyllites* Seward: Crane, 1985) could represent such plants. Alternatively, many advances (autapomorphies) of the angiosperms may not have evolved until the Cretaceous. Our scheme predicts that early members of the angiosperm line (like our hypothetical pro-anthophyte, Figure 2.2(*a*)) might be indistinguishable from Bennettitales in most characters commonly preserved in fossils – leaf morphology, stomata, wood anatomy, and pollen morphology – that is, in most respects other than nodal anatomy,
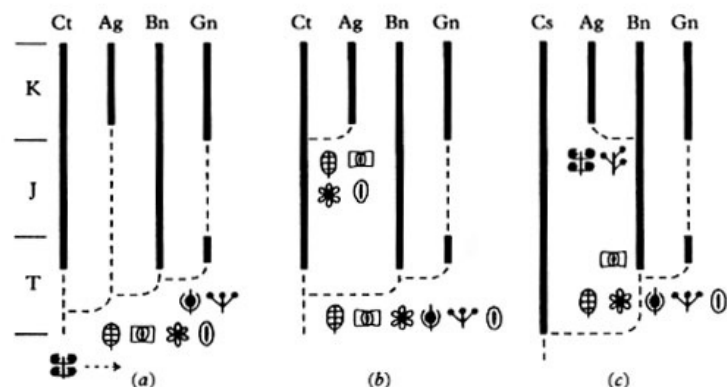
Figure 2.3. Alternative scenarios for the evolution of angiosperms and related groups. (a) Angiosperms as the sister group of other anthophytes, as in the most parsimonious cladograms (Figure 2.1, 123 steps); (b) angiosperms linked with *Caytonia* (124 steps); (c) angiosperms derived from some member of Bennettitales (consistent with some 125-step cladograms). 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 (a)): solitary orthotropus cupulate ovule; whorled microsporophylls; once-pinnate leaf; syndetocheilic stomata; sporophylls aggregated into flowers; granular monosulcate pollen; pinnate megasporophyll with anatropous cupulate ovules.

multicupulate megasporophylls, and spirally arranged microsporophylls (another idea anticipated by Arber & Parkin, 1907). This highlights the need for a search for reproductive structures associated with the many 'bennettitalean' genera that are known only as leaves. If the record of other adaptive radiations is any guide, a great variety of experimental anthophyte lines probably existed in the Triassic and Jurassic, of which the known groups are only the most common.

In almost equally parsimonious (124-step) cladograms with angiosperms linked with *Caytonia* (Figure 2.3 (b)), the reticulate venation and flat guard cells of the two groups are homologous rather than convergent, but simplified leaves, syndetocheilic stomata, granular pollen, and flowers originate independently in angiosperms and the bennettitalean-gnetalean line (or were lost in *Caytonia*). Presumably insect pollination, the ability to colonize unstable and/or arid habitats, and acceleration of the life cycle also arose independently in angiosperms and other

anthophytes. A weakness of this scheme is that most of the characters that potentially unite the anthophyte-*Caytonia* clade are unknown in *Caytonia*: not only presence of a tunica, lignin chemistry and siphonogamy, which are also undocumented in Bennettitales and *Pentoxylon*, but also scalariform pitting. However, this tree has the advantage of eliminating the stratigraphic gap in figure 2.3(a): since *Caytonia* is more primitive than angiosperms in all known characters, angiosperms could have evolved from some species of *Caytonia* at any time up to the Cretaceous.

As noted above, the next-best arrangement within the anthophytes links angiosperms directly with Bennettitales (125 steps). A closely related hypothesis that deserves special attention (Figure 2.3(c)) is that angiosperms were directly derived from some member of the Bennettitales, making Bennettitales a paraphyletic group. This would imply that angiosperms reverted to megasporophylls with several anatropous bitegmic ovules (cupules), spirally arranged microsporophylls, and no micropylar tube, and lost the few supposed autapomorphies of Bennettitales (unilacunar nodes, secretory canals, interseminal scales). However, this hypothesis would eliminate the stratigraphic gap in Figure 2.3(a). Since Bennettitales were a diverse group, recognition of special derived similarities between angiosperms and particular Bennettitales could make this alternative more parsimonious. Reinterpretations of basic conditions within angiosperms that would have the same effect are also conceivable. For example, we scored angiosperms as having multilacunar or trilacunar nodes, but nodal anatomy is diverse in magnoliids, and there is controversy over whether unilacunar, trilacunar or multilacunar nodes are ancestral (Bailey, 1956; Benzing, 1967; Takhtajan, 1969). Likewise, orthotropous ovules are typical of one magnoliid order, Piperales, including Chloranthaceae, which have pollen and leaves similar to some of the oldest Cretaceous angiosperms (Walker, 1976; Burger, 1977; Muller, 1981; Upchurch, 1984). The most implausible change required is derivation of carpels from stalked ovules, but S. V. Meyen (personal communication) suggested a speculative mechanism, gamoheterotopy, that might produce this result, parallel to the hypothesis that the ear of maize originated from the staminate inflorescence of teosinte, rather than the two-ranked pistillate inflorescence, by a regulatory mutation (Iltis, 1983). Some Bennettitales had leaf-like microsporophylls with microsynangia borne in two rows on the adaxial surface; extension of the developmental program for such

structures to the ovuliferous receptacle could result in flat megasporo-phylls with cupules substituted for microsynangia, like the hypothetical primitive carpel.

Since Gnetales have many of the same features that constitute obstacles to a bennettitalean origin of angiosperms, similar reinterpretations might also increase the plausibility of a direct relationship between angiosperms and Gnetales (Crane, 1985), now three steps less parsimonious than our best arrangement, especially if any additional 'gnetalean' features were reinterpreted as basic within angiosperms. Again, candidates for such characters exist in the Chloranthaceae (opposite leaves; swollen, two-trace nodes; inflorescences composed of small, apetalous flowers with uniovulate carpels). Gnetales have so many additional advances that derivation of angiosperms from Gnetales is highly unlikely. However, the two groups might both be derived from a bennettitalean line that began a trend for leaf simplification and floral reduction, which was continued in Gnetales but reversed in angiosperms.

These schemes help to put in clearer perspective possible causal factors in the origin of angiosperms. The scheme in which angiosperms are directly linked with *Caytonia* (Figure 2.3(b)) implies that the origin of flowers and acceleration of the life cycle occurred in the angiosperm line after its separation from its closest sister group and were therefore intimately tied with the origin of angiosperms, as assumed by Stebbins (1974), Doyle & Hickey (1976), and Doyle (1978, 1984). This would be consistent with suggestions that the origin of angiosperms from their immediate ancestors can be explained by paedomorphosis (Takhtajan, 1969), more specifically progenesis (Doyle, 1978). However, if angiosperms are the sister group of Bennettitales plus Gnetales (Figure 2.3(a)), which we consider most likely, or if angiosperms are derived from Bennettitales (Figure 2.3(c)), these same features originated earlier in the evolution of the anthophyte clade. Here the possible role of progenesis is more complex: some paedomorphic traits (gametophyte reduction, 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, reduced megaspore wall). This suggests that factors favoring progenesis were operating on the anthophytes since their origin, although they were continued and intensified 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, but that this tendency is strongest in early angiosperms and Gnetales. Similarly, insect pollination might be

proposed as a causal factor in the origin of angiosperms under the scheme in Figure 2.3(b), but under the others (Figure 2(a) and (c)) it was presumably established much earlier.

Under all three schemes, the closed carpel, stigmatic pollen germination, and double fertilization with endosperm formation arose only in angiosperms, whereas broad leaves with reticulate venation, vessels, simple microsporophylls, and reduced gametophytes evolved independently in angiosperms and Gnetales. All of these changes must be explained if the origin of angiosperms is to be understood. Where similar traits arose independently in angiosperms and Gnetales, comparisons between the two groups may clarify how and why such traits evolved. Thus the concentration of Early Cretaceous angiosperms and Gnetales in presumed seasonally arid tropical areas supports the idea that vessels originated as an adaptation to aridity, as suggested for Gnetales by Carlquist (1975). Once evolved, vessels may have been a preadaptation for evolution of large, undissected leaves in the tropics, since such leaves would tend to overheat even in wet tropical conditions unless vessels are present to allow rapid transpiration (Doyle *et al.*, 1982).

The implications of these results for factors in the rise of angiosperms are explored in detail by Doyle & Donoghue (1986b), on the basis of the idea that the relative diversity of clades is a function of speciation and extinction rates, and that some traits may have incidental effects on speciation rate, independent of why they evolved (Gould & Eldredge, 1977; Stanley, 1979; Vrba, 1983). Insect pollination might lead to higher speciation rates, by making possible pollinator-mediated isolating mechanisms, and to lower extinction rates, by allowing species to maintain more dispersed distributions of individuals and thus to escape herbivores and pathogens (Janzen, 1970; Regal, 1977; Stanley, 1979; Burger, 1981; Doyle *et al.*, 1982; Doyle, 1984; but see Stebbins, 1981). However, insect pollination probably existed in Bennettitales, Gnetales, and the angiosperm line itself since the Triassic. Possession of vessels and intercalary meristems (Stebbins, 1974, 1981), allowing leaf expansion, may have helped angiosperms to exploit tropical habitats more effectively, but the same features also arose in Gnetales. Some uniquely angiospermous trait(s) must be invoked to explain the Cretaceous expansion of angiosperms and their replacement of other anthophytes. We suggest that closure of the carpel may have played a key role, by raising speciation rates still higher. Carpel modifications for dispersal might lead to more frequent establishment of isolated populations, while stigmatic pollen germination might increase the probability that

mutations would result in incompatibility with pollen from partly differentiated populations. Since every new species represents an evolutionary experiment, high speciation rate alone might lead in the long term to occupation of more and more niches by angiosperms and their piecemeal replacement of other groups (Stanley, 1979; Doyle, 1984), independent of any superior features common to all angiosperms.

Although these scenarios are necessarily speculative and leave many questions unanswered, the analysis on which they rest greatly reduces the number of hypotheses on the origin of angiosperms that need to be seriously considered and makes a great number of detailed predictions that can be tested by future work. On the neontological front, a fruitful approach may be study of appropriate DNA sequences, which should show closer relationships between Gnetales and angiosperms than between any of the other major extant seed plant groups. On the palaeobotanical front, critical evidence could come from data on cryptic characters in Bennettitales (meristem type, lignin chemistry, embryology), stem anatomy and cupule orientation in *Caytonia* and other Mesozoic seed ferns, and morphological diversity within the anthophyte clade.

Appendix

Characters used by Doyle & Donoghue (1986b). 0 is used for the presumed ancestral state, 1 for the derived state, and X for missing information (see pp. 25–8). When only one state is listed, it is the derived state.

1. 0 = branching apical; 1 = axillary.
2. 0 = axillary buds single; 1 = multiple.
3. Leaves on (homologs of) progymnosperm penultimate order branches.
4. 0 = phyllotaxy spiral; 1 = opposite-decussate or whorled.
5–7. 000 = simple, dichotomous leaves only; 100 = pinnately compound leaves and cataphylls; 110 = simple (or dissected) pinnately veined leaves and cataphylls; X01, XX1 = simple, one-veined leaves only, or linear or dichotomous leaves and cataphylls.
8. 0 = rachis regularly bifurcate; 1 = usually or always simple.
9, 10. 00 = one order of laminar venation, open; 10 = one order of laminar venation, reticulate; 11 = two or more orders of laminar venation, at least one order reticulate.
11. 0 = poles of guard cells raised; 1 = level with aperture.
12. 0 = stomata entirely haplocheilic; 1 = some or all syndetocheilic.
13. Apical meristem with differentiation of tunica and corpus.
14, 15. 00 = protostele (including vitalized); 10 = eustele usually with external

secondary xylem only; X1 = eustele with regular internal secondary xylem.
16. 0 = some or all stem bundles mesarch or exarch; 1 = all endarch.
17, 18. 00 = leaf traces from one stem bundle or protoxylem strand (one-trace unilacunar); 10 = from more than two bundles (multilacunar); X1 = from two adjacent bundles (two-trace unilacunar).
19. 0 = some scalariform pits in metaxylem; 1 = no scalariform metaxylem, circular-bordered pits in protoxylem.
20. 0 = circular-bordered pitting or perforations only in the secondary xylem; 1 = at least some scalariform.
21. Vessels in the secondary xylem.
22. 0 = rays uniseriate, rarely biseriate; 1 = at least some multiseriate.
23. Secretory canals.
24. Mäule reaction.
25–27. 000 = dichotomous megasporangiate 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 sporophyll or sessile.
28–30. 000 = dichotomous microsporangiate appendages on radial axis; 100 = pinnately compound microsporophyll; 110 = once-pinnate microsporophyll, with two rows of simple leaflets or stalks bearing pollen sacs; X01, XX1 = one-veined microsporophyll.
31. 0 = ovule on lateral appendage; 1 = terminal.
32. 0 = homologs of progymnosperm fertile branchlets on homologs of lower-order axes; 1 = on homologs of last-order axes.
33–35. 000, 010 = ovule(s) in radial cupule; 100 = ovules directly on more or less laminar sporophyll; 110 = ovules in anatropous cupule, or anatropous and bitegmic; X01 = ovule with second integument derived from two appendages lower on axis.
36. 0 = several ovules per anatropous cupule or potential homolog; 1 = one.
37. 0 = microsporangia terminal, marginal, or adaxial; 1 = abaxial.
38. 0 = microsporangia free; 1 = more or less fused into microsynangia.
39. 0 = microsporophylls spirally arranged; 1 = whorled.
40. 0 = strobili on undifferentiated axes, or only female aggregated into compound strobili; 1 = both male and female strobili aggregated.
41, 42. 00 = no seeds; 10 = radiospermic seeds; X1 = platyspermic seeds.
43, 44. 00 = megasporangium with unmodified apex; 10 = lagenostome with central column; 11, X1 = pollen chamber without central column.
45. Micropylar tube.
46. Nucellar vasculature.
47. 0 = nucellar cuticle thin; 1 = thick, maceration resistant.
48. Heterospory.

49, 50. 00 = tetrad scar, no sulcus/pollen tube; 10 = sulcus/pollen tube; 11 = pollen tube but no sulcus.

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

52. 0 = pollen non-saccate or subsaccate; 1 = saccate.

53. 0 = infratectal structure alveolar; 1 = granular or columellar.

54. Pollen striate.

55. 0 = megaspore tetrad tetrahedral; 1 = linear.

56. 0 = megaspore wall thick; 1 = thin or lacking sporopollenin.

57. 0 = microgametophyte with prothallial(s) and sterile cell; 1 = prothallial but no sterile cell.

58. 0 = motile sperm; 1 = siphonogamy, non-motile sperm.

59. 0 = megagametophyte monosporic; 1 = tetrasporic.

60. Apex of megagametophyte free-nuclear or multinucleate; wall formation irregular, resulting in polyploid cells; egg a free nucleus.

61. 0 = early embryogenesis free-nuclear; 1 = entirely cellular.

62. Embryo with feeder.

Data matrix (Doyle & Donoghue, 1986 b).

```
                      1         2         3         4         5         6
Aneurophyton    0X00000X00XXX000000000X000000X0000X000000000XX000000000X00XXX
Archaeopteris   0X10000X00XXX100000000XX000000X1000X000000000XX100000000X00XXX
Multiov. lygin.ᵃ XX0010000000X0000000010X00000000000X010X101000X10000X000X000XX
Higher lygin.ᵇ  10001000000XX101000011X10010000000X010X101000X0000X000000000X
Medullosa       10001000000XX101000011X1001000010X010X101101X1001000X0X0X0XX
Callistophyton  1000100100X0X1000000010X10010000100011X0XX11100X1101100X00XX0XX
Glossopterids   10X0110X10X0X10XXXX00000XXX0X000X000000X1X10011101101X0XXX0XX
Peltaspermum    XX0X100100X0XXXXXXXXXX1010000100010OX111XX01101OX0X0XXXXX
Corystosperms   XX0010000000XX101000000X1001100011011100X111XX011011X0X1XXXXX
Caytonia        1000100X1010XXXXXXXXXXX1010000110OX10OX111001110110OX1XXXXX
Cycads          XXX0110X0000001011000011101X01X00X100X100X10X10101101000010000000
Bennettitales   10X0110X0001X101000011XXX11100X010X0110XXX110X11010101X00XX
Pentoxylon      10X0110X0000XX1XX101010XXX10100X010X0X10X1X100111010X0X1XXXXX
Cordaites       1010X01X0000X1000000000XX01X0101X00X0001X1X10X1000100000X0XX
Ginkgos         1010X01X00000101X1100000X01X101X00XX000X1X10001101000010000000
Conifers        1010X01X000001010010010X01X0101X00X1000X1X1000100110010000000
Ephedra         11X1XX1X0000110X1X1101101XX1XX11XX01X0111X110011110111101110010000
Welwitschia     11X1XX1X11010010X1X101111XX1XX01XX01X0111X1X1001101011X1111111
Gnetum          11X1110X1011101101X1X101X1XX11XX01X0X1110X11001110010X1111111
Angiosperms     10X0110X111111011001X1011101100X1101X100XXXX001110101011X10010
```

ᵃ Multiovulate lyginopterids.

ᵇ Higher lyginopterids.

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