12. Relationships of angiosperms and Gnetales: a numerical cladistic analysis

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Abstract

The significance of the numerous similarities between Gnetales and angiosperms has long been controversial, some considering them evidence of relationship, others as examples of convergence. A numerical cladistic (parsimony) analysis of seed plants plus progymnosperms supports the concept of Arber and Parkin, and Crane that angiosperms are related to Gnetales but not derived from them. Angiosperms are the sister group of Bennettitales and Gnetales, and gnetalian reproductive structures are best interpreted as highly reduced bennettitalian flowers. Although some angiosperm-gnetalian similarities (flowers, siphonogamy, tunica, lignin chemistry, reduced megaspore wall, granular exine) are probably homologous, others (vessels, dicot-like leaves, envelope around the seed, gametophyte reduction) are convergent. Computer experiments on modified data sets support the unity of the angiosperm–bennettitalian–gnetalian clade and the conclusion that coniferopsid characters of Gnetales are convergent. However, exact relationships with seed fern groups are more equivocal. Megafossils of Mesozoic Gnetales and better information on anatomy, chemistry, and embryology of Bennettitales and Caytoniales would provide further tests of relationships.

Introduction

The Gnetales (*Ephedra, Welwitschia, Gnetum*) are unique among gymnosperms in having so many features otherwise restricted to angiosperms (Martens 1971). 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. The significance of these similarities has long been a subject of controversy, some considering them evidence that Gnetales constitute a link between other gymnosperms and angiosperms, others considering them prime examples of convergence. Recent paleobotanical studies have added an ecological dimension to the parallels between angiosperms and Gnetales. Striate 'ephedroid' pollen comparable to *Ephedra* and *Welwitschia* in both general morphology and ultrastructure (Trevisan 1980) underwent a major Early Cretaceous radiation centered in the Northern Gondwana semiarid tropical belt, the same area where angiosperm pollen first appears and undergoes its most vigorous early diversification (Brenner 1976, Doyle *et al.* 1977, Doyle 1984); the two groups even tend to be abundant in the same local sedimentary facies (fluvial deposits: Doyle *et al.* 1982).

Previous ideas on relationships

Gnetales played a central role in Wettstein's (1907) theory of the origin of angiosperms, often associated with the Englerian school of systematics. Wettstein homologized the inflorescences of the wind-pollinated Amentiferae, made up of apetalous, unisexual flowers, with the compound strobili of Gnetales, and he interpreted the showy, bisexual flowers of magnoliids and other groups as pseudanthia derived by aggregation of unisexual units.

Arber and Parkin (1907, 1908) also believed that angiosperms and Gnetales are related, but they rejected Englerian concepts of angiosperm evolution, arguing that angiosperms, Gnetales, and the Mesozoic Bennettitales were derived from a hypothetical common ancestor with a bisexual pro-anthostrobilus. Thus they interpreted the 'flowers' of Gnetales as reduced from bisexual strobili rather than primitive (as they interpreted Amentiferae within angiosperms) citing among other evidence the presence of an abortive terminal ovule in the staminate flower of *Welwitschia*.

Views similar to those of Arber and Parkin have been expressed by Takhtajan (1969) and Ehrendorfer (1976), but in general the notion of a close relationship between angiosperms and Gnetales has fallen into disfavour. This is partly due to more thorough examination of characters and changing concepts of angiosperm phylogeny. Recognition of vesselless angiosperms suggested that angiosperms were derived from some group without vessels, not a group with them. Furthermore, vessel members appear to be derived from tracheids with different kinds of pitting in the two groups (scalariform in angiosperms, circular bordered in Gnetales: Thompson 1918, Bailey 1944). Increasing recognition of putatively ancestral characters in magnoliid dicots (vesselless wood, gymnosperm-like monosulcate pollen, leaflike carpels) and derived characters in Amentiferae (advanced vessels, triporate pollen) cast further doubt on Englerian views. More recently, palynological studies of Cretaceous rocks have shown that the first recognizable angiosperm pollen is monosulcate, while pollen of the amentiferous type does not appear until later, apparently as the culmination of a long series of modifications (reviewed in Doyle 1978).

Several lines of evidence have led to the idea that Gnetales are related to the so-called coniferopsid gymnosperms (conifers, ginkgos, cordaites) while angiosperms are related to cycadopsids (cycads, seed ferns, Bennettitales). For example, Gnetales have circular bordered pits in the metaxylem and even the protoxylem, like conifers and *Ginkgo*, but 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*, with the perianth of the staminate flower and the envelope around the seed both corresponding to the sterile scales below the stalk-like sporophylls. Eames rejected relationships of *Ephedra* with *Welwitschia* and *Gnetum*, largely on ontogenetic and anatomical arguments (not confirmed by more recent studies: Martens 1971) that the ovule is appendicular in *Ephedra* but truly terminal in *Gnetum* and *Welwitschia*, and that a shift from one condition to the other is impossible. He favoured relationships of *Welwitschia* and *Gnetum* with Bennettitales, partly because all three groups have syndetocheilic stomata (Florin 1931). However, others have noted that *Welwitschia* and *Gnetum* have the same coniferopsid wood features as *Ephedra* and that their reproductive structures can be interpreted in terms of the same basic plan (Bailey 1944, Bierhorst 1971, Doyle 1978). At the same time, closer connections have been proposed between angiosperms and specific cycadopsid groups. Thus angiosperm carpels have been homologized with the megasporophylls of Mesozoic seed ferns (*Caytonia*, Corystospermaceae), which bore reflexed cupules (equated with anatropous, bitegmic ovules) in two rows along the rachis, or with fertile structures of Permian glossopterids, which consisted of a leaf bearing one or more cupules on its adaxial surface (Gaussen 1946, Stebbins 1974, Doyle 1978, Retallack and Dilcher 1981). Since the recognition of the progymnosperms in the 1960's, it has been widely suggested that cycadopsids and coniferopsids were independently derived from Devonian progymnosperms (cycadopsids, some of which are protostelic, from the more primitive Aneurophytales; coniferopsids from more advanced types such as *Archaeopteris*: Beck 1981, Meeuse 1963). Taken together, these views would imply that angiosperms and Gnetales belong to evolutionary lines that have been separate since the Devonian.

Major doubts concerning aspects of this consensus have been expressed recently. Muhammad and Sattler (1982) found scalariform perforations in vessel elements of *Gnetum* and therefore questioned anatomical arguments against relationships between angiosperms and Gnetales, while Young (1981) argued on grounds of parsimony that the first angiosperms had vessels and these were lost in several early lines. Others have challenged the division of gymnosperms into cycadopsids and coniferopsids and the idea that the two groups were independently derived from progymnosperms. Thus Rothwell (1982) has documented remarkably coniferopsid-like characters in the Late Carboniferous seed fern *Callistophyton* (e.g. platyspermic ovules, saccate pollen) and has proposed that coniferopsids were derived from seed ferns by heterochronic substitution of scale leaves (cataphylls) for compound fronds, with concomitant changes in branching habit and stem anatomy. Meyen (1984) has proposed that cordaites and conifers are derived from one group of seed ferns (Lagenostomales) and ginkgos from another (Permian peltasperms, ultimately from Callistophytaceae).

Other challenges have come from cladistic studies of seed plant relationships. Cladistic analysis attempts to reconstruct the branching pattern of phylogeny (i.e. to recognize clades, or monophyletic groups in the strict sense of Hennig 1966) from the distribution of shared derived characters (synapomorphies), usually resolving character conflicts caused by convergence and reversal (homoplasy) on the principle of parsimony (i.e. preferring the hypothesis of relationships that requires the fewest character state changes, or steps). In an analysis that considered only extant groups, Hill and Crane (1982) favoured 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 contrasts with the conventional interpretation, which, rephrased in cladistic terms, would regard cycads as the sister group of angiosperms, and cycads plus angiosperms (cycadopsids in a broadened sense) as the sister group of coniferopsids (including *Ginkgo* and Gnetales). This analysis has subsequently been completely revised by Crane (1985), taking into account fossil as well as living groups. In agreement with Rothwell, he concludes that coniferopsids were derived from platyspermic seed ferns, but he separates Gnetales from the coniferopsids and places them together with angiosperms, Bennettitales, and *Pentoxylon* in a clade related to Mesozoic seed ferns.

The only way to resolve the question of angiosperm–gnetalian relationships and thus to determine whether their shared features are homologous or convergent is in the context of a general understanding of seed plant relationships, and we agree that the best approach to this goal is through cladistic analysis, as the most explicit and logically sound method of phylogeny reconstruction. However, cladistic studies on seed plants have so far been inconclusive. There is reason to suspect this is due in part to problems with the data and/or methods of analysis. For example, over half the characters used by Hill and Crane (1982) are apomorphies of all seed plants, of angiosperms or other terminal groups, or of Gnetales, and are therefore not informative in determining relationships among seed plant groups. Furthermore, many of the remaining characters are questionable, including the four used to support the proposed angiosperm–conifer–gnetalian clade: pycnoxylic anatomy is considered derived from manoxylic, but outgroup comparison with progymnosperms implies that it is actually ancestral (i.e. polarity was assessed incorrectly); siphonogamy and non–motile sperm are aspects of the same character (i.e. they are redundant); presence of strobili refers to structures made up of very different-looking parts in different groups. In addition, scoring of groups is sometimes questionable; e.g. angiosperms are scored as pycnoxylic, but primitive dicots have multiseriate rays and xylem parenchyma. (It should be noted that most of these problems were corrected in Crane's study.) Ideally, it should be possible to gain a synoptic picture of the total morphology of any terminal group by tracing the changes from the base of a cladogram to the top, but characters of leaf architecture, positional relationships of reproductive structures, and vegetative anatomy are poorly represented in Hill and Crane's data set. In addition, they did not take advantage of computer–assisted (numerical cladistic) methods, which are all but essential when dealing with large groups where character conflicts are common and where it is easy to overlook equally or even more parsimonious alternatives because of the burden of mental inertia.

In an attempt to understand why ideas on seed plant relationships differ so much from each other and to evaluate their relative merits, we undertook our own phylogenetic analysis, using numerical cladistic methods. Since our goal was to test current hypotheses, we made a great effort to code characters in ways that avoid bias for or against competing theories of character evolution. In order to assess the robustness of the results and the relative merits of alternatives, we also used the computer for a series of experiments, with variously modified data sets. More extensive documentation of our data matrix, justification of character coding and scoring of groups (which may sometimes seem to conflict with widely held assumptions), and discussion of broader implications will be presented elsewhere; here, we stress aspects of our study related to the angiosperm–Gnetales problem.

Methods of analysis

For cladogram construction we used the PHYSYS package of programs for phylogenetic analysis (Mickevich and Farris 1982, Smith *et al.* 1982), specifically the revised Wagner algorithm, which is improved over earlier versions in accepting missing data and in other respects. This algorithm begins with a matrix of binary characters, where 'zero' (0) normally represents the ancestral state and 'one' (1) the derived state, and attempts to find the branching diagram that minimizes the total number of character state transitions; it treats forward changes and reversals equally. In order to improve the chances of obtaining the most parsimonious tree(s), we used routines for global branch-swapping (WAG.S) and shuffling the order of entry of taxa (PIM). In a few cases we were able to obtain additional equally parsimonious trees by adding 'dummy' synapomorphies to force particular clades together and then subtracting the extra steps after analysis. This program provides diagnoses for terminal taxa and nodes that can be used to place characters on the tree, but often other arrangements of characters are equally parsimonious; in many cases, we preferred alternatives (e.g. origin and subsequent loss of a feature vs. two origins).

In our analysis, we attempted to represent all seed plant groups, but subdivision and inclusion of groups were necessarily a compromise based on a combination of factors, including a desire to recognize only monophyletic groups, the variable quantity and quality of information available, and relevance to competing theories of seed plant (especially angiosperm) relationships. Thus we treated the three modern genera of Gnetales separately because of recurrent controversy over whether they are related, and we included progymnosperms because of the possibility that seed plants are diphyletic. We split up several conventional taxa such as seed ferns because they are presumably paraphyletic (primitive grade taxa, some members of which are more closely related to various higher groups than to each other). Since many members of these groups are incompletely known, we represented them in the analysis with a few of the better-reconstructed forms (e.g. *Aneurophyton, Peltaspermum*). This procedure should not lead to misconceptions as long as it is realized, for example, that other 'Aneurophytales' may be cladistically more closely related to *Archaeopteris* or seed plants than to *Aneurophyton*. On the other hand, we left several large, diverse groups such as conifers and angiosperms undivided because they have enough apomorphies that they can be safely assumed monophyletic. In order to score such groups, it was necessary to determine basic conditions within them. In most cases these are clear from comparison with any plausible outgroup (e.g. monosulcate pollen in angiosperms), or from concepts of relationships within the group; often the results are corroborated by the stratigraphic record. Thus we used magnoliid dicots and pre-Albian fossils as guides in coding angiosperms, and Lebachiaceae in coding conifers.

Terminal taxa were scored for 62 binary characters (Tables 12.1,

Table 12.1: *Characters.* In the case of binary characters, only the derived state is given, or the ancestral state is also indicated in parentheses. In the case of multistate characters, the meaning of each coding is given.

1: axillary branching
2: accessory axillary buds
3: leaves on homologues of progymnosperm penultimate order axes
4: opposite phyllotaxy
5–7: 000 = all leaves dichotomous; 100 = pinnately compound leaves + cataphylls; 110 = simple or dissected leaves with pinnate venation + cataphylls; XX1 = linear or dichotomous leaves + cataphylls, or scale leaves only
8: rachis simple (vs. bifurcate)
9: finest vein order reticulate
10: several vein orders reticulate
11: guard cell poles level with aperture (vs. raised)
12: syndetocheilic stomata
13: tunica–corpus
14–15: 00 = protostele; 10 = eustele with internal secondary xylem; X1 = eustele with external secondary xylem only
16: all stem bundles endarch
17: each leaf supplied by >2 stem bundles
18: metaxylem without scalariform pitting
19: scalariform pitting in secondary xylem
20: vessels
21: multiseriate rays
22–23: 00 = no secretory cavities or canals; 10 = secretory cavities; X1 = secretory canals
24: Mäule reaction
25–27: 000 = megasporangia/ovules on dichotomous structures on radial axis; 100 = on pinnately compound sporophyll; 110 = on once-pinnate sporophyll (or simple but with lateral ovules); XX1 = on one-veined stalk or sessile
28–30: microsporangiate structures, same coding as 25–27
31: ovule terminal
32: fertile appendages on homologues of progymnosperm last order axes
33–35: 000 = ovule(s) in radial cupule; 100 = directly on ± planate sporophyll; X10 = in circinate cupule, or ovule bitegmic and anatropous; 101 = in second integument derived from two appendages
36: 1 ovule per radial cupule
37: 1 ovule per circinate cupule/ovule
38: microsporangia abaxial
39: microsporangia ± fused
40: microsporophylls whorled
41: compound male and female strobili
42–43: 00 = no seeds; 10 = radiospermic; X1 = platyspermic
44: lagenostome
45: micropylar tube
46: vascularized nucellus
47: thick nucellar cuticle
48: heterospory
49–50: 00 = tetrad scar, no sulcus; 10 = sulcus, pollen tube; 11 = pollen inaperturate
51: pollen bilaterally symmetrical
52: pollen saccate
53: exine granular (vs. alveolar)
54: striate exine sculpture
55: megaspore tetrad linear (vs. tetrahedral)
56: megaspore wall thin or lacking sporopollenin
57: microgametophyte with prothallial but no sterile cell
58: siphonogamy, non-motile sperm
59: tetrasporic megagametophyte
60: egg a free nucleus
61: early embryogenesis cellular
62: embryo with feeder

Table 12.2. Data Matrix

	1 2 3 4 5 6
Aneurophyton	0X00000X00---0000000000-000000X0XXXXXX0X0000XXX0000000XX-0XX--
Archaeopteris	0X10000X00---X1000000---000000X1XXXXX0000000XXX100000000-00X--
Pitus	--0010000000-0000000100-000000000000X010X10100-10000X000-000--
Lyginopterids	100010000000-0000000100-100100000001X010X10100-10000X000-000--
Medullosa	100010000000-10010001X1-10010000100XX010X10001-1001000-0-0-0--
Callistophyton	1000100100-0-X100000110-10010000100X0110XX1000-1101100-00--0--
Glossopterids	10X0110X10-0-X1-00000XX-XX0XX000100X0000XX100011101101-0---0--
Peltaspermum	--0-100100-0------------11010000100X0100XX10X-011010-0-0------
Corystosperms	--0010000000-1001000010-10011000X10X1100XX10X-011011-0-1------
Caytonia	--00100X1010------------11010000X10X0110XX100011101100-1------
Cycads	-XX0110X00000X1110001X101101100X100XX100X100010110100010000000
Bennettitales	10X0110X0001-X1100101X1-XX11100X0001X011X100100110101011--0--0
Pentoxylon	10X0110X0000-1000010100-XX10100X100XX0X1XX100--11010-0--------
Cordaites	1010XX1X0000-X100000010-X01X0101100XX0001X1001-1000100-000-0--
Ginkgos	1010XX1X00000X1101000100X01X0101100XX1000X10000110100010000000
Conifers	1010XX1X00000X1101000X10X01X0101100XX1000X10000100110010010000
Ephedra	11X1XX1X00001X1101011001XX1XX11X101XX0111X10100111101111010000
Welwitschia	11X1XX1X10010X11-1011X11XX1XX11X101XX0111X101001101011X1111111
Gnetum	11X1110X11011X1111111101XX1XX11X101XX0X111001001110010X1111111
Angiosperms	10X0110X11111X11101X10011101100XX10X1X10X100001110101011X10010

0: ancestral state; 1: derived state; -: information not available or questionable; X: not applicable (character not present), or precursor state unknown (in multistate characters).

12.2), of which 20 represent additive binary codings of eight multistate characters (cf. Brooks 1984). We made a great effort to amass potentially informative characters from all parts of the plant body, so as to give as complete a picture as possible of the morphology of terminal groups; 24 characters are vegetative, 38 reproductive. We did not include autapomorphies (derived characters unique to a single terminal taxon)—although autapomorphies are important in determining that the groups used are monophyletic, they contribute nothing to understanding relationships among groups, decrease the efficiency of computation, and give a false sense of the amount of information present in the matrix. We also attempted to eliminate redundant characters; sometimes these were recognized because they always changed simultaneously on cladograms obtained in preliminary analyses and could be plausibly attributed to the same morphogenetic factors (for example, loss of scalariform pitting in the metaxylem and presence of circular bordered pits in the protoxylem).

Polarities were determined by outgroup analysis (Maddison *et al.* 1984). Comparison of progymnosperms plus seed plants with Cladoxylales, sphenopsids, and ferns (the first outgroup) and trimerophytes (the second outgroup) indicated that *Aneurophyton* is primitive 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 and Wheeler 1981). On this basis, deciding on polarity and the resulting coding was often relatively easy (e.g. homospory to heterospory, free-sporing reproduction to seeds, 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 very different alternative interpretations on 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 favours one pathway. For example, under the hypothesis that cycadopsids and coniferopsids were separately derived from progymnosperms (Meeuse 1963, Beck 1981), the radiospermic seeds of cycadopsids and the platyspermic seeds of coniferopsids both originated from no seeds; under the hypothesis that coniferopsids were derived from platyspermic seed ferns (Rothwell 1982), all platyspermic seeds are derived from radiospermic. Thus binary coding no seeds '00', radiospermic '10', and platyspermic '11', which might be appropriate within seed ferns under either hypothesis, biases against the Beck–Meeuse hypothesis by making the transition from no seeds to platyspermic take two steps, while coding them '00', '10', and '01' adds an artificial step to a direct transition from radiospermic to platyspermic. In order to avoid such biases, we devised a new method of coding partially ordered characters which could take advantage of the algorithm's ability to deal with missing data ('X's' in the data matrix) by choosing whatever value for 'X' gives the most parsimonious result in combination with other characters. For example, we coded no seeds '00', radiospermic '10', and platyspermic 'X1' (i.e. either '01' or '11'): platyspermic can hence be derived from either no seeds or radiospermic by one step.

Similarly, we coded the coniferopsid leaf condition (scale leaves only, or scale leaves plus linear or dichotomous leaves) as 'XX1', so that it can be derived by one step from the condition in progymnosperms (dichotomous leaves only, '000'), in seed ferns (pinnately compound fronds and cataphylls, '100'), or in cycads (simply pinnate leaves and

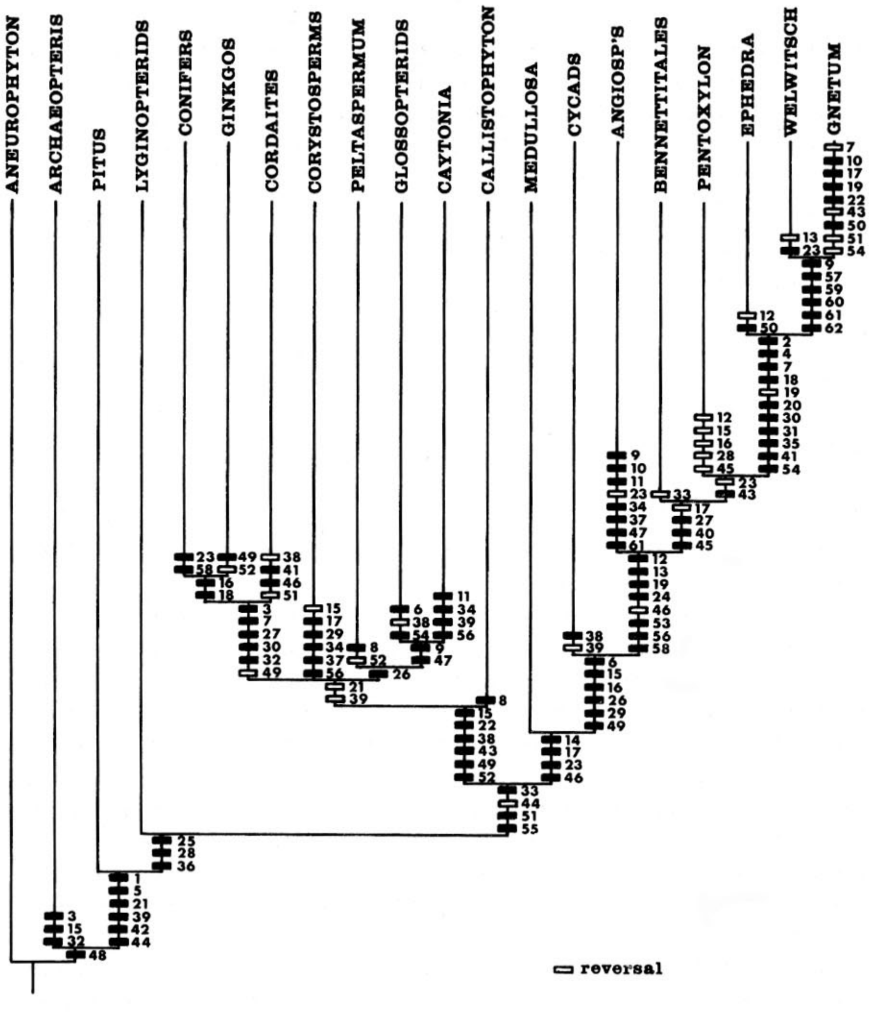

Fig. 12.1. One of four 130-step most parsimonious cladograms derived from the data matrix in Table 12.2.

cataphylls, '110'). As we will discuss in detail elsewhere, this technique does introduce a subtle, counterintuitive bias in some cases, by adding an artificial step when two or more groups with the X-coded state are positioned between groups with other codings in a cladogram, but this is not likely to pose a problem in the present case.

Results

Analysis of the data matrix in Table 12.2 resulted in four very similar most parsimonious cladograms requiring 130 character transitions. One of these is shown in Fig.12.1; how the others differ is discussed below. Lengths of the vertical internodes between branch points are proportional to the number of presumed synapomorphies, giving some idea of the relative support for particular connections. Since we excluded autapomorphies, characters on the lines leading to terminal taxa all change elsewhere on the tree, so they suggest the amount of homoplasy associated with the evolution of each terminal group.

At the base of the cladogram are a series of progymnosperms and Carboniferous seed ferns. *Aneurophyton* (including *Triloboxylon*) is primitive in all characters considered, while *Archaeopteris* is united with seed plants on heterospory (and possibly phloem structure: Wight and Beck 1984). The basal taxon within seed plants is the protostelic Early Carboniferous seed fern *Pitus*, reconstructed by Long (1979) as having pinnately compound leaves but multiovulate cupules on branch-like parts of a fertile frond, radiospermic seeds, microsynangia, and multiseriate rays. (A.C. Scott and G.W. Rothwell (personal communication) question Long's reconstruction of *Pitus*; however, because the characters of its supposed component parts are known in isolated organs of other early seed ferns and appear to be more primitive than those of later forms, we have retained Long's concept of *Pitus* in the analysis, as a plausible picture of the morphology of primitive seed ferns.) Lyginopterids in a strict sense (*Heterangium, Lyginopteris*), with planated fertile fronds and only one ovule per cupule, are the sister group of the remaining taxa, including all extant seed plants. These taxa form two major clades, united by lack of a cupule (possibly due to its transformation into a new integument) and lagenostome, bilaterally symmetrical pollen, and possibly a linear megaspore tetrad (the medullosan condition is controversial).

The basal taxon in one of the two clades is the late Carboniferous seed fern *Callistophyton*. Shared advances of this group (some lost in higher members) are a typical eustele, platyspermic ovules, saccate pollen, a sulcus and pollen tube, abaxial microsporangia, and secretory cavities;

since *Callistophyton* differs from the inferred ancestor in only one character (non-bifurcate rachis), we will refer to the whole group as the callistophyte clade. Besides *Callistophyton*, it includes not only the Mesozoic seed ferns, which have been associated with *Callistophyton* by several authors, but also glossopterids and coniferopsids. This generally supports Rothwell's (1982) view that coniferopsids originated from *Callistophyton*-like seed ferns rather than *Archaeopteris*-like progymnosperms. However, relationships within the clade are rather uncertain, probably because of poor information on characters in many groups. In Fig. 12.1, glossopterids and Mesozoic seed ferns are interpolated between *Callistophyton* and coniferopsids, based on their uniseriate rays and secondarily free microsporangia; this implies that the terminal microsporangia and radial pollen of cordaites and the lack of a sulcus in cordaites and primitive conifers (Mapes and Rothwell 1984) are secondary reversals. In one of the other 130-step trees, coniferopsids are the basal offshoot, and *Callistophyton* is nested well within the clade. In another, *Caytonia* and corystosperms together are placed below *Callistophyton*; according to this scheme, corystosperms are more primitive than other callistophytes in having a bifurcate rachis and probably medullosan stem anatomy (*Rhexoxylon*: Archangelsky 1968).

The basal member of the other clade is another late Carboniferous seed fern, *Medullosa*. The ancestor of this group could have been identical to *Medullosa*, with such advances as a eustele with internal secondary xylem, leaves supplied by traces from several primary xylem strands, secretory canals, and a vascularized nucellus. Excluding later modifications, the remaining members of this 'medullosan' clade are united by leaves with simply pinnate venation (either dissected, as in living cycads, or entire, as in *Taeniopteris*), a normal endarch eustele, once-pinnate sporophylls, and a sulcus. This group includes the cycads, which have often been considered medullosan derivatives, and a clade consisting of angiosperms, Bennettitales, *Pentoxylon*, and Gnetales. The fourth 130-step cladogram differs in reversing the order of Bennettitales and *Pentoxylon*, which does not significantly affect the results. Crane (1985) has proposed that the last four groups are related, but he links them with platyspermic seed ferns rather than cycads and medullosans. They are united by syndetocheilic stomata (lost in *Pentoxylon* and *Ephedra*), at least occasional scalariform pitting in the secondary xylem, granular exine structure, a reduced megaspore wall, and possibly several characters that are not preserved in Bennettitales or *Pentoxylon* but occur in both angiosperms and Gnetales: a tunica layer in the apical meristem, siphonogamy (which arises independently in conifers), and the Mäule reaction, an indication of lignin chemistry (Gibbs 1957).

Our results thus imply that Gnetales are the closest living relatives of angiosperms, but not that angiosperms were derived from (in cladistic terms, nested within) Gnetales, as proposed by Wettstein (1907). Instead, interrelationships of groups within the clade are more consistent with the scenario of Arber and Parkin (1908); that is to say, Gnetales are relatives of angiosperms and Bennettitales that underwent drastic floral reduction and aggregation in response to wind pollination, as did Amentiferae within angiosperms. Bennettitales and Gnetales share several advances over angiosperms—stalked or sessile ovules, whorled microsporophylls, and a micropylar tube—while the three genera of Gnetales are in turn united by opposite leaves (probably originally linear), multiple axillary buds, vessels, loss of scalariform pitting, simple microsporophylls, a single terminal ovule, a second integument apparently derived from the perianth of the ovulate flower, and striate pollen (lost in *Gnetum*). Within Gnetales, *Welwitschia* and *Gnetum* share additional advances over *Ephedra*: vein anastomoses, reduction of the male gametophyte, a tetrasporic megagametophyte with free nuclei serving as eggs, and a feeder in the embryo. Since the whole clade is related to groups with pinnately organized sporophylls, the angiosperm carpel can still be interpreted as a leaflike organ, while the solitary ovules of Bennettitales and Gnetales and the simple stamens of angiosperms and Gnetales are presumably reduced structures, as argued by Arber and Parkin. The fact that we obtained these results without assuming that the clade originally had bisexual strobili makes the agreements with Arber and Parkin all the more significant.

There are several reasons why these results should be treated with caution, and these should be considered before discussing additional implications. First, even our most parsimonious trees include a large amount of homoplasy—roughly one convergence or reversal per character. When homoplasy is common, many almost equally parsimonious arrangements can be expected, and the results may be unstable (sensitive to minor changes in interpretation of characters). Another reason for caution is that some of the strongest evidence for angiosperm–gnetalian relationships comes from chemical, embryological, and anatomical characters rarely preserved in fossils; one or more fossil groups may have had these (or other!) angiosperm apomorphies. Furthermore, although in general our results are gratifyingly consistent with the stratigraphic record, all the 130-step trees conflict at a few points with the known ranges of groups (e.g. cordaites extend down to the mid-Carboniferous, but none of their immediate sister groups in Fig. 12.1 are known before the Permian or Triassic, while the tree with coniferopsids at the base places *Callistophyton* among the younger groups). They also require morphological changes most would consider implausible (e.g. secondary loss of a sulcus and reappearance of a tetrad scar in coniferopsids, or reversion to synangia and multiseriate rays in

Callistophyton). Fortunately for our purposes, most such anomalies occur in the callistophyte clade and do not affect the question of angiosperm-gnetalian relationships.

To evaluate the nature and seriousness of these problems in more detail, we performed a series of experiments with modified data sets. We were able to determine lengths of many alternative trees by adding 'dummy' synapomorphies to the matrix to force particular relationships among taxa and then subtracting them from the resulting tree. Thus a tree in which coniferopsids are related to *Archaeopteris* (which would eliminate the reversals and stratigraphic anomalies mentioned above) is only two steps longer (132 steps) than the shortest trees; this suggests it would be premature to rule out the Beck–Meeuse hypothesis. Considering alternatives more directly relevant to the angiosperm–gnetalian question, trees in which Gnetales are forced into the coniferopsids are considerably longer (136 steps). However, when *Caytonia* and corystosperms are moved into the medullosan clade (which would fit the presumed medullosan anatomy of corystosperms), several trees of only 133 steps are obtained, some with cycads interpolated between *Caytonia* and corystosperms and angiosperms, others with angiosperms grouped with *Caytonia*. The best alternative found (132 steps) is obtained when angiosperms, Bennettitales, *Pentoxylon*, and Gnetales are moved into the callistophytes, as proposed by Crane, in which case they form part of a basal clade also including *Caytonia* and corystosperms. The last two alternatives are both consistent with the idea that the anatropous bitegmic ovules of angiosperms are homologous with *Caytonia* or corystosperm cupules. Trees in which the four groups are related to glossopterids are a little less parsimonious (134 steps); trees in which angiosperms alone are moved into the callistophytes are much worse (137 steps). We conclude that the exact relationships of angiosperms with seed fern groups are equivocal, and that several alternative theories on origin of the angiosperm carpel and bitegmic ovules (Stebbins 1974, Doyle 1978, Retallack and Dilcher 1981, Crane 1985) are still viable—but whatever the ultimate ancestry of angiosperms, their closest relatives are the Bennettitales and Gnetales.

As another test of the robustness of the results, we analysed subsets of the data matrix. Analysis of vegetative characters alone (1–24) separates Gnetales from Bennettitales and moves them into the coniferopsids; not surprisingly, angiosperms are associated with *Gnetum*. Analysis of macro-reproductive characters (25–43) also moves Gnetales into coniferopsids, but *Pentoxylon* and Bennettitales go with them, while angiosperms remain with cycads. When only micro-reproductive characters are analysed (44–62), the coniferopsids are broken up, while angiosperms, Bennettitales, and Gnetales form a clade related to Mesozoic seed ferns, as proposed by Crane, whose analysis emphasizes such characters. Removing nine characters which are rarely or never preserved in Mesozoic groups (13, 24, 55, 57–62) has relatively few effects on the results, perhaps the most interesting being that *Gnetum* is the basal taxon in Gnetales rather than *Ephedra*, underlining the importance of embryological characters in uniting *Welwitschia* and *Gnetum*. Significantly, none of these experiments broke up the Gnetales, as suggested by Eames (1952) and others. On the whole, these exercises support relationships among angiosperms, Bennettitales, and Gnetales, since either all three groups or pairs of them are linked in all cases.

Assuming that the results of our analysis of the whole data set are substantially correct, the links between Gnetales and coniferopsids in vegetative features (e.g. leaf morphology, anatomy) and between both Gnetales and Bennettitales and coniferopsids in macro-reproductive features (e.g. solitary ovules) are due to convergence. The fact that angiosperms too are nested within coniferopsids on vegetative data is largely attributable to convergence with Gnetales, especially *Gnetum*. Micro-reproductive features seem to give the most accurate indications of relationship, at least for the groups in question. It is easy to accept the macro-morphological similarities with coniferopsids as convergences, since most of them involve simple structures that may look similar simply because they are reduced. On the other hand, it is harder to imagine that many of the cycadopsid features of angiosperms (e.g. pinnately organized carpels) or Bennettitales (e.g. pinnate leaves) arose by convergence from a coniferopsid prototype: this would require elaboration of more complex structures, and it seems less likely that results similar to those in other groups would be obtained.

Critical re-examination of gnetalian structures often cited as indicating relationships with coniferopsids further supports our results. Thus Gnetales are like cordaites in having compound strobili consisting of bracts and axillary fertile shoots, but their microsporophylls are whorled and bear fused pollen sacs (except in *Gnetum*, which has only two sacs per flower), and their ovules have a micropylar tube and a reduced megaspore membrane, features anomalous in coniferopsids but typical of Bennettitales. Similarly, although Gnetales resemble conifers and *Ginkgo* in their pycnoxylic secondary xylem and lack of scalariform pitting in the primary xylem, they are like cycadopsids in having multiseriate rays.

Furthermore it appears, with hindsight, that several features which we excluded from the original data set because of uncertainty concerning polarity or homologies of parts may be additional synapomorphies of angiosperms, Bennettitales, and Gnetales. The three groups also show several striking parallel trends; these cannot be used as synapomorphies, but they may reflect shared genetic advances. For example, Ehrendorfer (1976) notes that Gnetales differ from other gymnosperms and resemble angiosperms in having relatively small chromosomes, less repetitive DNA, and extensive polyploidy. Although the ancestral condition in Bennettitales is controversial, our data are consistent with the idea that all three groups originally had flower-like bisexual strobili and a perianth, and hence that insect pollination was prevalent in the clade from its beginning. The three groups also show a strong tendency for adaptation to dry conditions: this is clearest from the Early Cretaceous record of angiosperms and Gnetales, but it is also true of Bennettitales, which were one of the dominant groups in southern Eurasia during the Late Jurassic, a period of widespread aridity (Vakhrameev 1970). These observations could greatly affect scenarios of early angiosperm evolution, since insect pollination, rapid reproduction, and ability to colonize arid or unstable habitats have been interpreted as key adaptations intimately associated with the origin of angiosperms and their occupation of a new adaptive zone (Stebbins 1974, Doyle and Hickey 1976, Doyle 1984). If these features arose earlier in evolution of the clade to which angiosperms belong, they cannot be the whole reason for the unique success of angiosperms.

Conclusions

The hypothesis that angiosperms are related to Bennettitales and Gnetales considerably simplifies some aspects of angiosperm evolution, by reducing the number of changes required in the origin of the group. For example, it implies that the angiosperm flower is a structure with direct homologues in related groups, and the same can be said of the essentially bennettitalian wood anatomy, stomatal structure, and granular monosulcate pollen of primitive angiosperms. However, it does leave unanswered some of the problems that have most vexed botanists, particularly the origin of the carpel, since ovulate structures of Gnetales and Bennettitales are so reduced that evidence on basic sporophyll morphology must be sought in more distant relatives. It also provides no obvious explanation for origin of the second integument in angiosperms, although a cupule of some sort is known in Triassic Bennettitales (Harris 1932, Crane this volume). Both problems might be alleviated if new evidence associates the angiosperm–bennettitalian clade with *Caytonia* and corystosperms, an alternative that is already nearly as parsimonious (see Addendum to this Chapter).

Our results may make the origin of angiosperms somewhat less mysterious in another way, since they imply that the angiosperms were a product of the radiation of one of the most vigorous Mesozoic groups, rather than the final offshoot of a declining seed fern line. On the other hand, derivation of angiosperms and Bennettitales from a common ancestor implies that the angiosperm line existed at least as far back as Bennettitales (i.e. Late Triassic) whereas convincing angiosperm remains are not known until the Cretaceous. One explanation is that angiosperms were geographically or ecologically restricted before the Cretaceous. However, it is also possible that many typical advances of angiosperms did not evolve in the angiosperm line until the Cretaceous. Our scheme predicts that leaves, wood, and pollen of early angiosperm precursors (in fact, all but floral structures) might be easy to mistake for remains of Bennettitales (cf. Arber and Parkin 1907).

Our analysis also clarifies why angiosperm–gnetalian relationships have been so controversial. Previous workers were quite right in interpreting many striking similarities between the two groups as convergences, but they were incorrect in assuming that this ruled out all relationships. Thus, even if Young (1981) is right that vessels are ancestral in angiosperms, vessels presumably arose independently in the two groups, since they are absent in Bennettitales and *Pentoxylon*. Positional relationships of floral parts imply that the envelope around the seed in Gnetales is homologous with the perianth of Bennettitales (and presumably angiosperms), not the carpel wall. Judging from conditions in *Ephedra*, Bennettitales, and *Pentoxylon*, the dicot-like leaves of *Gnetum* and the reduced gametophytes of *Gnetum* and *Welwitschia* arose within Gnetales. Most of the chemical similarities between Gnetales and angiosperms noted by Gottlieb and Kubitzki (1984) are presumably also convergent, since they occur in the 'rosiflorean block' which appears to be nested within higher dicots on such advances as triaperturate pollen. The real homologies are more cryptic (siphonogamy, tunica-corpus, lignin chemistry, reduced megaspore wall, granular exine) and their significance is difficult to recognize except in the context of broader relationships, particularly when Gnetales are viewed as highly derived relatives of Bennettitales.

In addition, many arguments concerning angiosperm–gnetalian relationships have been clouded by questionable phylogenetic reasoning. Perhaps most importantly, the question has often been phrased in terms of whether or not Gnetales could be ancestors of angiosperms (e.g. Bailey 1944, Doyle 1978, Muhammad and Sattler 1982) which overlooks the possibility that they were derived from a common ancestor that would not be placed in either group. Many workers, particularly Eames, were guilty of extreme character weighting, elevating minor morphological distinctions (some of them probably imaginary, like ovule position in different Gnetales) to insurmountable obstacles to relationship, and dismissing characters as systematically worthless because they arose independently elsewhere. Although we have found much independent support for the conclusions of Arber and Parkin, it is easy to dismiss their original arguments as excessively speculative.

One of the great strengths of cladistic analysis is that it makes so many predictions to be tested by future work. On the neontological front, molecular data might provide valuable tests. Under our hypothesis, angiosperms probably diverged from Gnetales as recently as the Triassic, while all other connections among major extant seed plant groups would date at least to the Carboniferous; such a difference in divergence time might be detected by studies of appropriate DNA sequences. On the paleobotanical front, critical evidence might come from information on cryptic characters of Bennettitales (meristem type, lignin chemistry, embryology), to determine whether they have the predicted gnetalian–angiosperm conditions, and on diversity within the group, as stressed by Crane (this volume). Data on missing characters of Mesozoic seed ferns and organs of Mesozoic Gnetales other than pollen could also be critical. There are a few incompletely known megafossils that may be gnetalian, such as the Late Triassic genus *Dechellyia* (Ash 1972), which was conifer-like in habit but had opposite leaves and is associated with cones containing ephedroid pollen. If future work on *Dechellyia* reveals other apomorphies of Gnetales but not the bennettitalian features of the modern genera, it might support the coniferopsid alternative. On the other hand, Early Cretaceous gnetalian megafossils under study by Upchurch and Crane (1985) have loosely organized reproductive structures, supporting the idea that the compound strobili of modern Gnetales are aggregations of bennettitalian flowers rather than structures inherited from cordaites.

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Addendum

Since completing this study, we reanalysed our data matrix with revised codings of certain characters. Our primary purpose was to take into account the evidence presented by Crane (this volume) that *Pentoxylon* had a radial cupule and that Bennettitales may have been primitively platyspermic. In the process, we also discovered a subtle bias against Crane's (1985) hypothesis that the clade consisting of angiosperms, Bennettitales, *Pentoxylon*, and Gnetales is most closely related to

Mesozoic seed ferns with circinate cupules. As mentioned in the text, the use of X-coding in multistate characters biases against placement of X-coded taxa between taxa with different codings. However, under the present coding of the cupule character (33–35), Crane's hypothesis requires just this sort of arrangement, since it postulates that circinate cupules ('X10') were intermediate between leaf-borne, non-cupulate seeds ('100') and radial cupules ('000'). The computer counts this transformation series as three steps (1→0 in binary character 33, 0→1→0 in 34), one more than the actual number of morphological changes involved. We removed this bias by recoding non-cupulate seeds '100', circinate cupules '110', orthotropous cupules of Bennettitales and *Pentoxylon* '010', and the gnetalian condition 'X01'. To express the uncertainty concerning basic seed symmetry in Bennettitales and angiosperms (where the seeds are too reduced to show the usual criteria of symmetry, such as bundles in the inner integument), we re-coded both groups 'XX' for this character (42–43).

Mega- and microsporophylls of cycads (25–27, 28–30) differ greatly from those of other groups coded as once-pinnate, in bearing ovules directly on the rachis and pollen sacs scattered on either side of the midrib, rather than on leaflet-like segments. Since these observations suggest that cycad sporophylls may have been reduced from pinnately compound structures by a unique pathway, we recoded both 25–27 and 28–30 as '1XO', which treats derivation from pinnately compound or via once-pinnate intermediates as equally likely.

With these changes, trees in which the angiosperm-bennettitalian-gnetalian clade is related to Mesozoic seed ferns (*Caytonia*, corystosperms, and/or glossopterids) become two or three steps *more* parsimonious than trees in which it is related to cycads and medullosans. As noted in the text, such relationships have the advantage of providing homologues for the second integument of angiosperms and the cupule of Bennettitales and *Pentoxylon*, which have no obvious precursor structures in the schemes reported above.

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