

CHAPTER 13

Phylogenetic studies of seed plants and angiosperms based on morphological characters

MICHAEL J. DONOGHUE¹ and JAMES A. DOYLE²

¹ Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, U.S.A. and ² Department of Botany, University of California, Davis, CA 95616, U.S.A.

Introduction

The origin of angiosperms (flowering plants) is a perennial topic of debate in evolutionary biology. Morphological trends and homologies in seed plants ('gymnosperms' and angiosperms) have been widely discussed, but a variety of alternative phylogenetic theories have persisted, and there have been few constraints on the development of evolutionary scenarios (e.g., [1]). This we believe is largely because most discussions have proceeded in the absence of clearly stated phylogenetic hypotheses based on the totality of character evidence [2].

Recently, there have been several cladistic analyses of the relationships of angiosperms to other seed plants and among primary lines in angiosperms. Here we summarize results of these studies, especially our own analyses based on morphological characters [3,4]. We emphasize implications for the development of a phylogenetic system of seed plants and congruence of trees based on morphological and molecular data; relations to macro-evolution have been treated elsewhere.

Seed plant phylogeny

It has long been suggested that seed plants consist of two independent lines – cycadopsids (cycads and 'seed ferns') and coniferopsids (conifers, ginkgos, cordaites). This idea gained support from work on Devonian 'progymnosperms', which lacked seeds but resembled seed plants anatomically. Beck [5] argued that cycadopsids were derived from one group of progymnosperms ('aneurophytes') by planation of branch systems into compound fronds, coniferopsids from another (*Archaeopteris*) by leaf reduction. If so, the seed itself originated twice, which is consistent with its different

symmetry in the two lines – basically radial (radiospermic) in cycadopsids, bilateral (platyspermic) in coniferopsids. However, this diphyletic concept has been challenged by Rothwell [6], based primarily on the Carboniferous seed fern *Callistophyton*, which had platyspermic seeds, saccate pollen, and other conifer-like features. To explain the drastic transformation in leaf morphology required in deriving coniferopsids from a *Callistophyton*-like plant, Rothwell invoked heterochronic suppression of fronds and continued production of scale leaves. If this idea applies to all coniferopsids, it implies that seed plants are monophyletic. Meyen [7] also argued that all seed plants were derived from seed ferns, but he envisioned two separate platyspermic lines, Pinopsida (conifers and cordaites) and Ginkgoopsida (ginkgos, platyspermic seed ferns, etc.).

Even more controversy surrounds the relationships of angiosperms. Von Wettstein [8] interpreted the wind-pollinated, catkin-bearing Amentiferae as primitive and derived angiosperms from the extant order Gnetales. In contrast, Arber and Parkin [9,10] interpreted *Magnolia* and similar forms (now classified as Magnoliidae) as primitive and derived angiosperms, Gnetales, and Mesozoic Bennettitales from a common ancestor with showy, bisexual strobili, implying that the minute flowers of both Amentiferae and Gnetales are reduced. Subsequent recognition of many gymnosperm-like features in magnoliids, such as monosulcate pollen and vesselless wood, tended to confirm the view that magnoliids are primitive and Amentiferae derived; it is also supported by recent studies of the Early Cretaceous fossil record [11]. However, most recent authors have rejected relationships with either Bennettitales or Gnetales. Bennettitales have been dismissed because their ovules are borne singly on stalks that are difficult to homologize with the angiosperm carpel, while Gnetales have been separated from angiosperms and associated with coniferopsids on the basis of their wood anatomy, linear leaves, and compound strobili. More attention has been focused on Permian and Mesozoic seed ferns (glossopterids, corystosperms, *Caytonia*), which have pinnately organized sporophylls with ovule-bearing cupules that can be homologized with the anatropous, bitegmic ovules of angiosperms [1,11,12]. However, angiosperms have been linked with almost every other group at some time, and some authors envision a polyphyletic origin from several lines [13,14].

Cladistic analyses

The first concerted effort to assess cladistic relationships among seed plants was that of Hill and Crane [15]. These authors concluded that angiosperms are probably most closely related to conifers plus Gnetales and that together these are related to cycads plus *Ginkgo*. However, this analysis was limited because it considered only extant groups, omitted many potentially informative characters, and did not analyze the data numerically [3].

Crane [16,17] greatly extended this analysis, taking into account fossil groups, making major improvements in character analysis, and using a Wagner parsimony algorithm. Despite these improvements, we were initially unconvinced by his results. For example, he concluded that seed plants are monophyletic, with coniferopsids

linked with *Callistophyton*, Mesozoic seed ferns, and other groups in a 'platysperm' clade characterized by platyspermic seeds and saccate pollen – consistent with the views of Rothwell. However, his analysis did not adequately test the monophyly of seed plants: he included only one 'progymnosperm', coded platyspermic seeds as derived from radiospermic, and omitted several vegetative similarities between coniferopsids and *Archaeopteris*. Crane's most original conclusion was that angiosperms, Gnetales, Bennettitales, and the Mesozoic genus *Pentoxylon* form a clade (termed 'anthophytes' because they all have flower-like strobili) nested among Mesozoic seed ferns. As he noted, this reconciles Arber and Parkin's [9,10] concept that angiosperms are related to Bennettitales and Gnetales and proposed homologies between angiosperms and Mesozoic seed ferns. However, his data set did not include widely cited similarities between Gnetales and coniferopsids. Finally, the robustness of his results and the relative parsimony of alternative hypotheses were not investigated.

Our own analyses of seed plant phylogeny [3] were undertaken to provide an independent test of Hill and Crane [15] and later Crane [16], and to evaluate critically a wide range of alternative phylogenetic theories. For this purpose we assembled a much larger set of potentially informative characters, representing all parts of the plant body. We tried to minimize bias for or against competing morphological theories by using an 'X-coding' method of coding partially ordered multistate characters, which has since been superseded by direct coding methods. We included two progymnosperm groups in order to test the monophyly of seed plants. Finally, we explored the robustness of our results and the parsimony of alternative arrangements in a series of computer experiments.

Basic seed plant relationships

Despite our inclusion of potentially contradictory characters and liberal coding methods, our findings (Fig. 1) are largely congruent with Crane's. Thus they support the view that seed plants are a monophyletic group derived from (nested within) 'progymnosperms'. The first seed plants would be typologically classified as lyginopterid seed ferns, with frond-like leaves and radiospermic ovules. As in Crane's trees, coniferopsids are nested within seed plants, in a clade characterized by platyspermic seeds and saccate pollen, which also includes *Callistophyton*, Mesozoic seed ferns, and anthophytes. Thus, both analyses indicate that coniferopsids are monophyletic but 'cycadopsids' are paraphyletic. Meyen's [7] division of platysperms into Pinopsida and Ginkgoopsida is substantially less parsimonious (adding at least 25 steps).

Although this was the most parsimonious arrangement (123 steps), we found trees in which coniferopsids are directly united with *Archaeopteris* that were only one step longer. We were therefore reluctant to reject Beck's [5] hypothesis that seed plants are diphyletic. However, in retrospect, the view that seed plants are monophyletic seems stronger than our analysis indicated. First, we were trying to be as fair as possible to both theories – perhaps excessively so. For example, we included similarities in leaf and sporophyll distribution in *Archaeopteris* and coniferopsids that might arise automati-

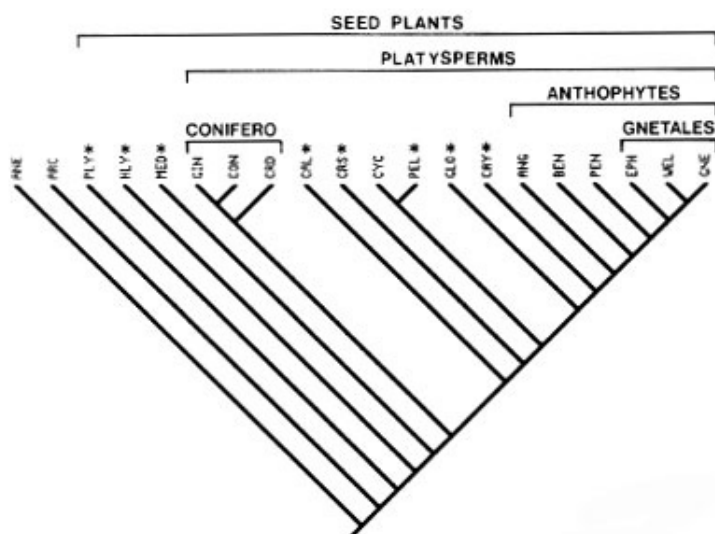


Fig. 1. Representative most parsimonious cladogram of seed plants and 'progymnosperms' [3], with major monophyletic groups indicated by brackets and the paraphyletic 'seed ferns' marked by asterisks. 123 steps (consistency index = 0.50), based on 62 binary characters (including multistate characters coded in binary form). Abbreviations of taxa: ANE: *Aneurophyton* s. l.; ARC: *Archaeopteris*; PLY: protostelic lyginopterids; HLY: 'higher' lyginopterids (*Heterangium*, *Lyginopteris*); MED: *Medullosa*; CON: Coniferales; GIN: Ginkgoales; CRD: Cordaitales; CAL: *Callistophyton*; CRS: Corystospermaceae; CYC: Cycadales; PEL: *Peltasperмум*; GLO: Glossopteridales; CAY: *Caytonia*; ANG: angiosperms; BEN: Bennettitales; PEN: *Pentoxylon*; EPH: *Ephedra*; WEL: *Wielwitschia*; GNE: *Gnetum*.

cally during derivation of a coniferopsid branching pattern from a seed fern pattern. Elimination of these characters would weaken a connection between coniferopsids and *Archaeopteris* (and among coniferopsids themselves, perhaps allowing Meyen's placement of ginkgos with peltasperms). Second, we omitted several characters that would favor placement of coniferopsids among seed ferns: e.g., differentiation of the integument into sclerotesta and sarcotesta layers in *Medullosa*, *Callistophyton*, cordaites, and ginkgos; presence of mucilage cavities in *Callistophyton*, corystosperms, cordaites, and *Ginkgo*; and seed characters used by Crane that we rejected as redundant, such as one functional megaspore.

Relationships among groups within the platyspermic clade vary greatly in strength. Coniferopsids and anthophytes are well supported, but there are several equally or almost equally parsimonious arrangements of the remaining groups. The position of cycads is especially problematical. Although they are linked with peltasperms in Fig. 1 (which requires a reversion to radiospermic seeds), it is equally parsimonious to unite them with *Medullosa* or interpolate them between *Medullosa* and platysperms, as in Crane's trees. We now incline toward the view that cycads belong among the platysperms, which would then include all extant seed plants. First, Permian taeniopterids, which had megasporophylls suggestive of cycads, were apparently platyspermic, and

Cycas seeds are bilaterally symmetrical, supporting the notion that the first cycads were actually platyspermic. Second, the alveolar exine structure of cycads appears to be more advanced than that of *Medullosa* and more like that of coniferopsids and platyspermic seed ferns [18]. Finally, Pigg [19] has shown that petiole anatomy was similar in corystosperms and cycads but different in medullosans.

Anthophyte relationships

Our study also identifies an 'anthophyte' clade consisting of angiosperms, Bennettitales, *Pentoxylon*, and Gnetales, which (excluding later reversals) is united by scalariform secondary xylem pitting, loss of air sacs in the pollen, granular exine structure, and a variety of other features. The exact arrangement of related groups differs in our scheme and in Crane's, but this is not a major conflict. In our trees the closest relatives of anthophytes are *Caytonia* and glossopterids, whereas Crane linked them with corystosperms; however, trees of the two kinds differ by only one or two steps. Furthermore, both schemes imply that the bitegmic ovules of angiosperms and the orthotropous cupules of Bennettitales and *Pentoxylon* are homologous with the reflexed cupules of some Mesozoic seed fern group, as first proposed by Crane [16].

Within anthophytes, our results are more at odds with Crane's. His trees link angiosperms directly with Gnetales, whereas in ours angiosperms are the sister group of the remaining anthophytes, which are united by erect, solitary ovules, whorled microsporophylls, and possibly a micropylar tube. Given our data set, Crane's arrangement is three steps less parsimonious. Although these two topologies have some similar implications (e.g., that the angiosperm line, though not necessarily all angiosperm apomorphies, must have existed long before the Cretaceous radiation), there are also significant differences. For example, our scheme implies that angiosperm carpels are directly homologous with the multicupulate megasporophylls of *Caytonia*, whereas Crane's requires either independent reduction of megasporophylls in Bennettitales and Gnetales, or secondary multiplication and reorientation of ovules (cupules) in angiosperms.

The Gnetales are one of the best supported clades in both analyses, despite the extreme morphological differences among the three extant genera. Unifying features include opposite leaves, circular bordered pits in the protoxylem, vessels, simple microsporophylls, one terminal ovule, and compound strobili; linear leaves and striate pollen may also have been present in ancestral Gnetales and reversed in *Gnetum*. Although some of these features are also shared by coniferopsids, it requires at least four additional steps to unite Gnetales with coniferopsids, and 11 more steps to unite *Ephedra* alone with coniferopsids [20]. Within Gnetales, *Welwitschia* and *Gnetum* are linked by advances in leaf venation and embryology. Although some of these traits are shared with angiosperms, at least 10 extra steps are required to link angiosperms directly with *Welwitschia* and *Gnetum*. Thus, although Gnetales are the closest living relatives of angiosperms, neither group is 'derived from' the other, and most of the features cited as evidence for a relationship between them probably arose independently.

Based on these results, some traditional groups are paraphyletic rather than monophyletic – for example, progymnosperms, gymnosperms, cycadopsids, and seed ferns – and should be eliminated from the phylogenetic system [21]. However, the monophyly of other traditional groups is supported, such as seed plants, coniferopsids, and Gnetales. Cladistic studies have also identified clades that have not been recognized previously, notably platysperms and anthophytes.

Angiosperm phylogeny

Although theories that angiosperms are polyphyletic persist [13,14], their monophyly is supported by at least nine morphological characters, including sieve tubes and companion cells derived from the same initials, stamens with two pairs of pollen sacs, trinucleate male gametophytes, closed carpels with stigmatic pollen germination, eight-nucleate female gametophytes (or related conditions), and double fertilization associated with endosperm formation [3]. Although we therefore assumed that angiosperms are monophyletic, this could be tested cladistically by adding several potentially unrelated angiosperm groups to a seed plant data set. A polyphyletic origin would require that all the traits listed above evolved independently; it is extremely doubtful that similarities between angiosperms and different gymnosperm groups could overcome this cost.

Most recent authors accept that the 'Magnoliidae' include the most primitive angiosperms, but there is much disagreement over details, in part because of conflicts among characters. Some consider Magnoliaceae and related families most primitive, stressing their monosulcate pollen and granular exine structure [22]; others Winteraceae, emphasizing their vesselless wood [23]. In addition, more unorthodox concepts are far from dead. For example, Burger has suggested that the most primitive angiosperms are Piperales and/or Chloranthaceae, which have unusually simple flowers but pollen remarkably like some of the earliest Cretaceous angiosperms [24], or that monocots are basal [25], rather than derived from herbaceous magnoliids such as Nymphaeales or Piperales [26].

Another recurrent controversy concerns whether the basically tricolpate groups ('higher dicots') are mono- or polyphyletic, and which magnoliid groups are their closest relatives. Takhtajan [27] postulated three tricolpate lines, all derived independently from Magnoliales: Hamamelidae, representing an early trend toward wind pollination; Illiciales, Ranunculidae, and Caryophyllidae; and Rosidae, Dilleniidae, and Asteridae. Emphasizing leaf characters, Hickey and Wolfe [28] proposed that Illiciales, Ranunculidae, and Hamamelidae are related to Chloranthaceae, and that Hamamelidae are in turn linked with Rosidae. Emphasizing pollen characters, Walker and Walker [22] linked Hamamelidae, Rosidae, and Dilleniidae with Chloranthaceae and Piperales, implying that higher dicots passed through an evolutionary phase with reduced flowers, but they associated Illiciales and Ranunculidae with Winteraceae.

Cladistic analyses

There have been a few previous cladistic analyses of basal angiosperm relationships, but the resulting trees show little congruence with each other or with our results, apparently due to basic deficiencies in the data and/or methods of analysis. The study of Young [29] suffered from problems in treatment of multistate characters and variability within taxa, polarity assessment, inclusion of taxa, and inadequate efforts to find most parsimonious trees [30]. Dahlgren and Bremer [31] found a very large number of equally parsimonious trees, with few characters supporting major clades, leaving great uncertainty over the robustness of the results. The study of Lammers et al. [32], which was aimed at resolving the systematic position of *Lactoris*, attempted first to identify related taxa by a phenetic analysis and then analyzed these (Magnoliales) plus *Lactoris* cladistically; judging from our results, this led them to exclude the closest relatives of *Lactoris* from their cladistic analysis.

Our own study [4] emphasized the position of the Hamamelidae, but it was intended as an analysis of all angiosperms. Some large groups such as monocots were treated as units, and certain plesiomorphic tricolpate taxa (Ranunculidae, Trochodendrales, Hamamelidales) were included as 'placeholders' for derived groups (based in part on a preliminary study by Donoghue [33]). We built directly on our seed plant study in using the inferred relationships of angiosperms to other anthophytes and *Caytonia* as a basis for polarity assessment within angiosperms, which allowed us to polarize 30 out of 54 characters. When a character varied within a taxon, we either tried to determine the basic state or scored the character as 'unknown'. Analyses were done with PAUP [34], supplemented by MacClade [35], which was especially useful in exploring implications of alternative topologies. One of our most parsimonious trees (178 steps) is shown in Fig. 2; variations among shortest trees will be noted where appropriate.

Angiosperm clades

In Fig. 2, seven families of Cronquist's [36] Magnoliales (those that retain granular exine structure) form a basal clade; in other trees, Canellaceae, *Eupomatia*, and Himantandraceae are variously associated with the remaining groups. Under both of these rooting hypotheses, the rest of the angiosperms are united by columellar exine structure and endexine, with exceptions (core Laurales, Nymphaeales) best interpreted as reversals.

The 'columellate' clade consists of three groups that form an unresolved trichotomy; however, each of them is fairly well supported. One corresponds to Laurales in a broad sense, united by opposite leaves and unilacunar nodes. Chloranthaceae are securely nested in Laurales, near Trimeniaceae, as argued by Endress [37]; their widely proposed alternative positions, in Piperales or as a link between Piperales and Laurales, are at least seven steps worse. The second clade ('winteroids') consists of Winteraceae and the tricolpate order Illiciales (cf. Walker and Walker [22]); this arrangement implies that the lack of vessels in Winteraceae (and all other vesselless groups) is due to secondary loss (cf. Young [29]).

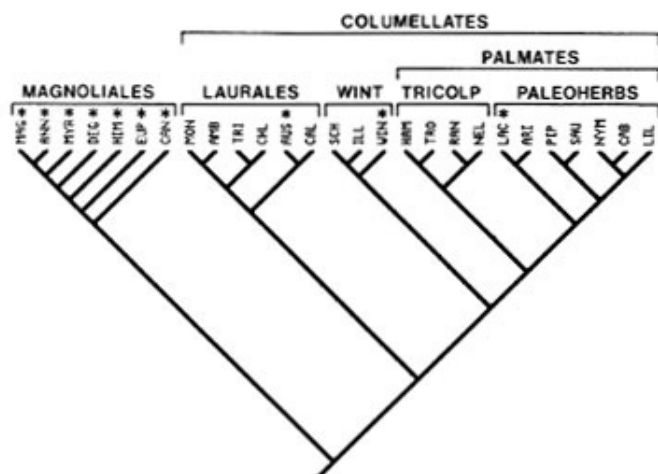


Fig. 2. Representative most parsimonious cladogram of angiosperms [4], with major monophyletic groups indicated by brackets and the paraphyletic Magnoliales of Cronquist [36] marked by asterisks. 178 steps (consistency index = 0.39), based on 54 characters (42 binary, 12 unordered multistate; 69 minimum possible steps). Abbreviations of taxa: MAG: Magnoliaceae; ANN: Annonaceae; MYR: Myristicaceae; DEG: Degeneriaceae; HIM: Himantandraceae; EUP: Eupomatiaceae; CAN: Canellaceae; MON: Monimiaceae s. l., Gomortegaceae, Hernandiaceae, Lauraceae; AMB: Amborellaceae; TRI: Trimeniaceae; CHL: Chloranthaceae; AUS: Austrobaileyeaceae; CAL: Calycanthaceae; SCH: Schisandraceae; ILL: Illiciaceae; WINT: Winteraceae; HAM: Hamamelidales; TRO: Trochodendrales; RAN: Ranunculidae; NEL: Nelumbonaceae; LAC: Lactoridaceae; ARI: Aristolochiaceae; PIP: Piperaceae; SAU: Saururaceae; NYM: Nymphaeaceae; CAB: Cabombaceae; LIL: Liliopsida (monocots).

Our most original result is recognition of the third columellate clade ('palmates'), which includes herbaceous magnoliids and monocots ('paleoherbs') and most tricolpate dicots, united by palmate leaf venation (and derived conditions) and stamens with well-differentiated filaments. In most trees, Trochodendrales plus Hamamelidales are united with Ranunculidae plus *Nelumbo* (often placed in Nymphaeales), based on loss of ethereal oil cells and tricolpate pollen. However, some trees link Ranunculidae and *Nelumbo* with the paleoherbs, based on herbaceous habit and anomocytic stomata. If the former trees are correct, and if Rosidae, Dilleniidae, and Caryophyllidae are linked with Hamamelidales [22,28,33], all triaperturate dicots except Illiciaceae form a single clade (contrary to Takhtajan [27]).

Another novel result is recognition of the paleoherb clade, united by basically two perianth cycles and trimery in both perianth and androecium. Arrangements within this clade are not well resolved, but Nymphaeales (minus *Nelumbo*) are always the sister group of monocots, as widely proposed. However, it also includes the Piperales (Piperaceae, Saururaceae), sometimes also linked with monocots. Piperales are one of our strongest clades, unequivocally supported by six characters. Placement of Aristolochiaceae and *Lactoris* in the paleoherbs contradicts Lammers et al. [32] but was anticipated by Dahlgren and Bremer [31].

We treated the monocots as a unit, but the assumption that they are monophyletic

is not well established and should be tested in future studies. Many of the characters normally associated with monocots occur in other paleoherbs, and given the position of monocots within this group, they are not necessarily synapomorphies of monocots alone. It is therefore conceivable that monocots originated more than once within this clade; indeed, they arose twice in the preliminary analysis of Donoghue [33], which included an alismid, an aroid, and a dioscorid.

The greatest uncertainty concerns rooting of the angiosperm tree, due primarily to difficulties in polarizing characters based on outgroup analysis. With the present data set, it is most parsimonious to root angiosperms in or next to Magnoliales; however, we found several radically different trees, with angiosperms rooted next to or among the paleoherbs, that are only one or two steps worse. In the best of these (179 steps), Nymphaeales are basal, monocots are linked with Piperales, and tricolpates are interpolated between the two clades. This recalls the views of Burger [25]; however, the shortest trees with monocots themselves basal are 183 steps, and placing the root within monocots would presumably add more steps corresponding to monocot advances (e.g., one cotyledon). Contrary to standard views, trees rooted among paleoherbs imply that palmate venation, anomocytic stomata, and filaments are primitive in angiosperms; we were unable to polarize these characters by outgroup comparison. It should be noted that not all alternative views on rooting are so parsimonious; for example, trees rooted next to Chloranthaceae are at least seven steps longer.

Considering implications for a phylogenetic system of the angiosperms, our results support retention of the Laurales and identify several previously unrecognized clades, such as columellates, paleoherbs, and tricolpates. However, dicots and Magnoliidae are paraphyletic and should be abandoned. The Magnoliales of Cronquist [36] are also paraphyletic, since some of the component taxa are basal or near-basal members of other clades: *Austrobaileya* in the Laurales, Winteraceae in the winteroids, *Lactoris* in the paleoherbs. However, some or all of the remaining Magnoliales (those with granular exines) may be monophyletic. It should also be noted that the almost equally parsimonious rooting among the paleoherbs would significantly alter a phylogenetic system. In particular, paleoherbs, palmates, and columellates would become paraphyletic. However, the tricolpates, winteroids, Laurales, and Magnoliales would be monophyletic. These observations underline the critical importance of resolving the position of the root.

Congruence with molecular cladograms

At first sight, our results show little congruence with cladograms based on molecular data. However, closer examination suggests that most of the incongruence results from different levels of resolution of particular relationships by one or another type of data, consistent with generalizations of Hillis [38]. Genuine conflicts, where morphological data strongly support one alternative and molecular data strongly support another, are the exception.

Martin and Dowd's results based on 40 amino acids of rubisco (ribulose 1,5-bisphosphate carboxylase/oxygenase) [39] deviate considerably from ours. For example, they conclude that *Ginkgo* is the sister group of angiosperms, while *Ephedra* is more closely related to conifers (*Metasequoia*). However, their earlier analysis [40] agreed with ours in linking *Ephedra* with angiosperms. Within angiosperms the root is next to Illiciales, ranunculids are split up, Ranunculaceae are linked with Nymphaeaceae and Cabombaceae, monocots are united with Piperaceae and *Nelumbo*, and some (but not all) Magnoliales are nested in Laurales. These results are highly unpar-simonious morphologically: although we cannot evaluate their tree in detail owing to differences in the taxa considered, any cladogram that reflects its basic features requires at least 205 steps in terms of our data (ca. 15% more than our shortest trees). One problem is that Martin and Dowd's method of adding the results of a series of analyses of conventionally defined taxa may have yielded trees that are not globally parsimonious. More critical, however, is the fact that the data themselves may be too limited. It is difficult to evaluate the robustness of the rubisco trees because the character support is not shown, but other analyses of amino acid sequences for angiosperms, including rubisco, show little congruence among most parsimonious trees [41]. Similar results have been obtained for amino acid data sets in mammals [42]. This may be because there are too few variable sites, and these show high levels of homoplasy [41].

Our results are somewhat more consistent with the ribosomal RNA data of Zimmer et al. [43; personal communication], judging by their experiments with alternative topologies. For example, both data sets indicate that seed plants, Gnetales, and angiosperms are monophyletic groups, supported by many characters of both sorts. The most parsimonious rRNA trees (1296 steps) link angiosperms with a conifer-ginkgo-cycad clade, rather than with Gnetales. However, trees with Gnetales as the sister group of angiosperms are only three steps (0.2%) longer, and analysis of the rRNA data using the evolutionary parsimony method of Lake [44] confidently unites the two groups. Similarly, Piperaceae and Saururaceae are weakly separated based on rRNA data but strongly united based on morphology. These may be cases in which the morphological data provide better resolution.

Most disconcerting from a conventional point of view is the result that monocots arose polyphyletically from widely separated dicots, with *Sagittaria* united with Fabaceae and *Potamogeton* with Winteraceae (Zimmer, personal communication). As noted above, monocots arose twice in a preliminary morphological analysis [33], but both origins occurred within the paleoherb clade. The more extreme rRNA arrangement would be much less parsimonious morphologically: it implies that the many features uniting *Sagittaria* and *Potamogeton* with both monocots and other paleoherbs are homoplastic, and that features uniting Fabaceae and other 'higher' dicots (tricolpate pollen, pentamerous flowers, etc.) were lost in *Sagittaria*. If the polyphyly of monocots persists as molecular data accumulate, this would constitute a genuine conflict, indicating substantial homoplasy in molecular and/or morphological characters.

Another difference concerns the rooting of the angiosperms. In the shortest rRNA trees, angiosperms are rooted between monocots (aroids and grasses) and dicots (with Piperales and Nymphaeales basal), rather than in or near Magnoliales. Zimmer et al. report that trees rooted near 'magnoliids' are at least 37 steps worse, although they may not have tested all appropriate topologies. On the other hand, it should be recalled that our own conclusions on rooting were weak, and in fact we found arrangements only one or two steps longer than our best trees that are rooted in or next to the paleoherbs. If these results hold up, this may be a case in which molecular data provide better resolution than morphology.

We see several possibilities for resolving the rooting problem. In terms of morphology, analysis of more fossil anthophyte taxa together with several basic angiosperm clades might allow simultaneous resolution of outgroup and ingroup relationships and thereby identify the globally most parsimonious position of the root [45]. However, unless angiosperms are nested within anthophytes, as in Crane's [16] scheme or Meyen's [46] hypothesis that angiosperms are derived from Bennettitales, major progress may require discovery of new plesiomorphic anthophyte taxa or early offshoots of the angiosperm line itself, with some but not all of the apomorphies of extant angiosperms. Such fossils are likely to have the most effect on the position and internal topology of groups with numerous apomorphies, such as angiosperms [47,48]. The Triassic plants described by Cornet [49] are especially promising in this regard (e.g., they resemble angiosperms in having bilocular pollen sacs). Finally, we are optimistic that additional molecular data will provide more decisive results. This is most likely if any extant angiosperm lines (whether monocots, Nymphaeales, or some group of 'Magnoliales') diverged well before the main radiation of angiosperms in the Cretaceous.

Acknowledgements

We are grateful to the Nobel Symposium organizing committee, and especially to K. Bremer, for inviting us to participate. We also thank E. Zimmer and P. Martin for providing access to their unpublished data.

References

- 1 Stebbins GL. Flowering Plants: Evolution Above the Species Level. Cambridge: Harvard University Press, 1974.
- 2 Eldredge N, Cracraft J. Phylogenetic Patterns and the Evolutionary Process. New York: Columbia University Press, 1980.
- 3 Doyle JA, Donoghue MJ. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot Rev* 1986; 52: 321–431.

- 4 Donoghue MJ, Doyle JA. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. In: Crane PR, Blackmore S (Eds.) *Evolution, Systematics, and Fossil History of the Hamamelidae*. Oxford: Clarendon Press, 1989.
- 5 Beck CB. *Archaeopteris* and its role in vascular plant evolution. In: Niklas KJ (Ed.) *Paleobotany, Paleocology, and Evolution*, Vol. 1. New York: Praeger, 1981; 193–230.
- 6 Rothwell GW. New interpretations of the earliest conifers. *Rev Palaeobot Palynol* 1982; 37: 7–28.
- 7 Meyen SV. Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record. *Bot Rev* 1984; 50: 1–112.
- 8 von Wettstein RR. *Handbuch der systematischen Botanik*, Band II. Leipzig: Franz Deuticke, 1907.
- 9 Arber EAN, Parkin J. On the origin of angiosperms. *J Linn Soc Bot* 1907; 38: 29–80.
- 10 Arber EAN, Parkin J. Studies on the evolution of the angiosperms. The relationship of the angiosperms to the Gnetales. *Ann Bot* 1908; 22: 489–515.
- 11 Doyle JA. Origin of angiosperms. *Annu Rev Ecol Syst* 1978; 9: 365–392.
- 12 Retallack G, Dilcher DL. Arguments for a glossopterid ancestry of angiosperms. *Paleobiology* 1981; 7: 54–67.
- 13 Meese ADJ. Facts and fiction in floral morphology with special reference to the Polycarpicae. *Acta Bot Neerl* 1972; 21: 113–127, 235–252, 351–365.
- 14 Krassilov VA. The origin of angiosperms. *Bot Rev* 1977; 43: 143–176.
- 15 Hill CR, Crane PR. Evolutionary cladistics and the origin of angiosperms. In: Joysey KA, Friday AE (Eds.) *Problems of Phylogenetic Reconstruction*. London: Academic Press, 1982; 269–361.
- 16 Crane PR. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann Missouri Bot Gard* 1985; 72: 716–793.
- 17 Crane PR. Phylogenetic relationships in seed plants. *Cladistics* 1985; 1: 329–348.
- 18 Taylor TN, Zavada MS. Developmental and functional aspects of fossil pollen. In: Blackmore S, Ferguson IK (Eds.) *Pollen and Spores: Form and Function*. London: Academic Press, 1986; 165–178.
- 19 Pigg KB. *Corynosperms* from the Triassic of Antarctica: *Dicroidium*. *Am J Bot* 1988; 75 (6, Part 2): 114.
- 20 Eames AJ. Relationships of the Ephedrales. *Phytomorphology* 1952; 2: 79–100.
- 21 Donoghue MJ, Cantino PD. Paraphyly, ancestors, and the goals of taxonomy: a botanical defense of cladism. *Bot Rev* 1988; 54: 107–128.
- 22 Walker JW, Walker AG. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Ann Missouri Bot Gard* 1984; 71: 464–521.
- 23 Thorne RF. A phylogenetic classification of the Annoniflorae. *Aliso* 1974; 8: 147–209.
- 24 Burger WC. The Piperales and the monocots: alternative hypotheses for the origin of monocotyledonous flowers. *Bot Rev* 1977; 43: 345–393.
- 25 Burger WC. Heresy revived: the monocot theory of angiosperm origin. *Evol Theory* 1981; 5: 189–225.
- 26 Dahlgren RMT, Clifford HT, Yeo PF. *The Families of the Monocotyledons. Structure, Evolution, and Taxonomy*. Berlin: Springer-Verlag, 1985.
- 27 Takhtajan AL. Outline of the classification of flowering plants (Magnoliophyta). *Bot Rev* 1980; 46: 225–359.
- 28 Hickey LJ, Wolfe JA. The bases of angiosperm phylogeny: vegetative morphology. *Ann Missouri Bot Gard* 1975; 62: 538–589.
- 29 Young DA. Are the angiosperms primitively vesselless? *Syst Bot* 1981; 6: 313–330.
- 30 Riggins R, Farris JS. Cladistics and the roots of angiosperms. *Syst Bot* 1983; 8: 96–101.
- 31 Dahlgren R, Bremer K. Major clades of the angiosperms. *Cladistics* 1985; 1: 349–368.
- 32 Lammers TG, Stuessy TF, Silva OM. Systematic relationships of the Lactoridaceae, endemic family of the Juan Fernandez Islands, Chile. *Plant Syst Evol* 1986; 152: 243–266.
- 33 Donoghue MJ. Phylogenetic analysis and the angiosperm system. XIV Internat Bot Congr (Berlin) Abstr, 1987; 281.
- 34 Swofford DL. *PAUP: Phylogenetic Analysis Using Parsimony, Version 2.4*. Champaign: Illinois Natural History Survey, 1985.

- 35 Maddison WP, Maddison DR. MacClade, version 2.1. A phylogenetics computer program distributed by the authors, 1987.
- 36 Cronquist A. An Integrated System of Classification of Flowering Plants. New York: Columbia University Press, 1981.
- 37 Endress PK. The Chloranthaceae: reproductive structures and phylogenetic position. *Bot Jahrb Syst* 1987; 109: 153–226.
- 38 Hillis DM. Molecular versus morphological approaches to systematics. *Annu Rev Ecol Syst* 1987; 18: 23–42.
- 39 Martin PG, Dowd JM. Phylogeny among the flowering plants as derived from amino acid sequence data. In: Fernholm B, Bremer K, Jönvall H (Eds.) *The Hierarchy of Life*. Amsterdam: Elsevier, 1989; 195–204.
- 40 Martin PG, Dowd JM. A phylogenetic tree for some monocotyledons and gymnosperms derived from protein sequences. *Taxon* 1986; 35: 469–475.
- 41 Bremer K. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 1988; 42: 795–803.
- 42 Wyss AR, Novacek MJ, McKenna MC. Amino acid sequence versus morphological data and the interordinal relationships of mammals. *Mol Biol Evol* 1987; 4: 99–116.
- 43 Zimmer EA, Hamby RK, Arnold ML, LeBlanc DA, Theriot EC. Ribosomal RNA phylogenies and flowering plant evolution. In: Fernholm B, Bremer K, Jönvall H (Eds.) *The Hierarchy of Life*. Amsterdam: Elsevier, 1989; 205–214.
- 44 Lake JA. A rate-independent technique for analysis of nucleic acid sequences: evolutionary parsimony. *Mol Biol Evol* 1987; 4: 167–191.
- 45 Maddison WP, Donoghue MD, Maddison DR. Outgroup analysis and parsimony. *Syst Zool* 1984; 33: 83–103.
- 46 Meyen SV. Origin of the angiosperm gynoecium by gamoheterotopy. *Bot J Linn Soc* 1988; 97: 171–178.
- 47 Doyle JA, Donoghue MJ. The importance of fossils in elucidating seed plant phylogeny and macroevolution. *Rev Palaeobot Palynol* 1987; 50: 63–95.
- 48 Gauthier J, Kluge AG, Rowe T. Amniote phylogeny and the importance of fossils. *Cladistics* 1988; 4: 105–209.
- 49 Cornet B. The leaf venation and reproductive structures of a Late Triassic angiosperm, *Saunmiguella lewisii*. *Evol Theory* 1986; 7: 231–309.