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Introduction and 'Lower' Hamamelidae

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3. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae

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Abstract

In order to explore the basal radiation of angiosperms and the phylogenetic position of 'Hamamelidae', we conducted a numerical cladistic analysis of monosulcate taxa ('Magnoliidae', monocots) and six tricolpate groups (assumed to be appropriate placeholders for 'Rosidae', 'Amentiferae', and other 'higher dicots'). Based on outgroup comparison with Bennettitales plus Gnetales and with Mesozoic seed ferns, angiosperms are best rooted either within Magnoliales or with Magnoliales forming a basal clade. The remaining angiosperms are united by columellar exine structure. Within this group there are three main clades: i) Laurales, including *Austrobaileya*, Calycanthaceae, Trimeniaceae, and Chloranthaceae; ii) Winteraceae plus Illiciales; and iii) a group united by palmate leaf venation and differentiated stamen filaments, which contains the tricolpate groups (except Illiciales) and a 'paleoherb' clade consisting of *Lactoris*, Aristolochiaceae, Piperaceae plus Saururaceae, Nymphaeaceae plus Cabombaceae, and monocots. Within the palmate clade, Trochodendrales plus Hamamelidales and Ranunculidae plus *Nelumbo* may form a clade united by tricolpate pollen and loss of ethereal oil cells, or Ranunculidae and *Nelumbo* may be linked with the paleoherbs based on anomocytic stomata and herbaceous habit. Under both arrangements the chloranthoid teeth of Chloranthaceae are not homologous with those in Hamamelidae and Ranunculidae, but there are almost equally parsimonious

trees in which they may be homologous. Studies of Early Cretaceous cordate leaves and tricolpate pollen and of living paleoherb groups could provide valuable tests of these results. In future cladistic studies of Hamamelidae and other 'higher' dicots, Ranunculidae and paleoherbs should be considered closer outgroups than Magnoliales or Chloranthaceae.

Introduction

The position of the predominantly wind-pollinated groups assigned to the 'Hamamelidae' has long been a controversial issue in angiosperm phylogeny. Although the older view that 'Amentiferae' (i.e. 'higher hamamelids') are primitive angiosperms is now generally dismissed, there is still debate on whether Hamamelidae are a natural group or independent derivatives of diverse entomophilous ancestors, and whether their reduced flowers and anemophily are 'dead end' specializations or typical of an intermediate phase in the evolution of 'higher dicots' from monosulcate 'Magnoliidae' (cf. Ehrendorfer Vol. 40A, Ch. 1).

In our view, progress in unraveling these questions depends critically on understanding phylogenetic relationships at the base of the angiosperms. Although it is generally agreed that magnoliids are most similar to the first angiosperms (a view supported by the fossil record: Doyle 1969, 1978; Wolfe *et al.* 1975; Hickey and Doyle 1977), there remain major uncertainties on relationships among magnoliids, the course of character evolution, and ecological trends. Although most workers consider Winteraceae or Magnoliaceae most primitive, some suggest that Chloranthaceae or monocots are basal (e.g. Burger 1977, 1981), and there is little agreement on exactly how higher dicots are related to magnoliids. This is due in part to uncertainty on the relationships of angiosperms as a whole, and hence the polarity of character evolution within the group. However, this situation has improved as a result of recent cladistic analyses of seed plants (Crane 1985; Doyle and Donoghue 1986), which provide much more robust conclusions on the relationships of angiosperms to other groups.

In this paper, building on our seed plant study, we present a preliminary numerical cladistic analysis designed to resolve relationships at the base of the angiosperms, and consider its bearing on the phylogenetic position of Hamamelidae. We cannot address all aspects of this question, since this would require an analysis of many hamamelid groups and all of their potential relatives, which would be impractical at the present time. Instead, we will concentrate on analyzing relationships of presumably primitive hamamelids in the context of monosulcate

groups and several tricolpate groups that are thought to be basal members of other higher dicot lines. Although this analysis is preliminary and incomplete, we hope that it will serve to point the way to a more complete solution. The present description of our analysis is necessarily abbreviated; detailed justification of the inclusion of taxa and the choice and coding of characters will be presented elsewhere.

Background

One popular view of hamamelid relationships is that of Takhtajan (1966, 1980, 1987) and Cronquist (1968), who considered Hamamelidae to be a natural group derived directly from magnoliids, parallel to other major groups (rosids, dilleniids, caryophyllids, monocots). They interpreted Hamamelidae as products of an early trend toward increasing anemophily, with Trochodendrales and Hamamelidales (which have presumably primitive features such as tricolpate pollen and, in Trochodendrales, vesselless wood) occupying an intermediate position between magnoliids and Amentiferae (most of which have triporate pollen). This contrasts with the schemes of Thorne (1968, 1976) and Dahlgren (1975, 1983), in which Hamamelidales and Fagales are thought to be derived from magnoliids but are also related to groups classified by Takhtajan and Cronquist as rosids, and other hamamelid groups are derived from unrelated triaperturate ancestors (e.g. Thorne placed Juglandaceae in Rutales, Urticales in Malviflorae). All of these authors left open the critical question of which magnoliid groups are most closely related to hamamelids.

One of the first attempts to link hamamelids with specific magnoliids was that of Hickey and Wolfe (1975), based on leaf architecture. Among their major contributions was the recognition of several marginal tooth types, defined on form, venation, and glandularity. Most interesting for our purposes is the chloranthoid tooth, with two lateral veins joining the medial vein and a glandular papilla, which they noted in several tricolpate groups—Illiciales, Ranunculales, and a few 'lower' Hamamelidae (*Trochodendron, Tetracentron, Cercidiphyllum*)—and in the magnoliid family Chloranthaceae. The Chloranthaceae, which contrast with most magnoliids in having extremely simple flowers, have been considered reduced Laurales, members of the Piperales (with which they share minute flowers, spicate inflorescences, and orthotropous ovules), or transitional between the two. The presence of chloranthoid teeth led Hickey and Wolfe to associate Chloranthaceae with Illiciales, Ranunculidae, and Hamamelidae. They argued that lower hamamelids are in turn linked with Rosidae, based primarily on similarities between Early

Cretaceous palmately lobed platanoid leaves (believed to be hamamelids) and pinnately lobed and compound *Sapindopsis* leaves (believed to be primitive rosids).

Pollen morphology has been another source of recent ideas on magnoliid–hamamelid relationships. Walker and Walker (1984) inferred a general trend within magnoliids from large, boat-shaped monosulcate pollen with a complete tectum and granular infratectal structure, to small, round monosulcate pollen with an open (semitectate), reticulate tectum, and columellar infratectal structure, which in turn gave rise to tricolpate pollen. Looking in more detail, they proposed two links between monosulcate and tricolpate groups. One was between the basically tricolpate Illiciales (*Illicium*, Schisandraceae) and Winteraceae (with monoulcerate tetrads), both of which have a coarse reticulum of peaked muri supported by short columellae. They also included Aristolochiaceae in this group, based on the reticulate monosulcate pollen of *Saruma*. The other proposed link was between Hamamelidae and Chloranthaceae plus Piperales (which they dissociated from Laurales), based on the spinulose muri and sculptured apertures of Chloranthaceae and some lower hamamelids (*Cercidiphyllum*, *Euptelea*). They noted that these conclusions are generally consistent with the chloranthoid tooth character, although their scheme would imply that chloranthoid teeth arose independently in Illiciales. They also argued that lower hamamelids are transitional to rosids and dilleniids, implying that the showy flowers of the latter groups are secondarily elaborated from reduced, apetalous flowers.

These indications of a closer connection between Hamamelidae and Rosidae were acknowledged by Cronquist (1981), who also noted supporting chemical evidence (cf. Kubitzki 1973). They are also reflected in Ehrendorfer's concept (Vol. 40A, Ch. 1) that Hamamelidae form a 'transitional field' between Magnoliidae and higher dicots. However, we caution against viewing the Hamamelidae as a single unit in this regard; most of the evidence for a transitional status concerns tricolpate Trochodendrales and Hamamelidales and does not necessarily apply to triporate Juglandales, Betulales, and Urticales, which may instead be nested within rosids or dilleniids.

Recently new evidence has appeared on the magnoliid group most widely discussed in connection with Hamamelidae, the Chloranthaceae. In a study emphasizing reproductive characters, Endress (1987) found that Chloranthaceae share the greatest number of similarities with Trimeniaceae, then with *Amborella*, then with other Laurales, and the fewest with Piperales. These observations suggest that Chloranthaceae are nested within Laurales and cast doubt on a direct relationship between Chloranthaceae and either Hamamelidae or Piperales, since this would require reversal of several lauralean advances (e.g. opposite

leaves, unilacunar nodes, uniovulate carpels). However, this argument does not rule out the homology of chloranthoid teeth or the possibility that hamamelids and Laurales are sister groups: Endress (1987) noted chloranthoid teeth in Trimeniaceae, and we have seen them in *Amborella* (based on a photograph kindly provided by J. A. Wolfe).

We believe that the best way to resolve such diverse opinions on relationships and apparent conflicts among character sets is through parsimony analysis, attempting to determine which phylogenetic hypothesis best accounts for the totality of character information. There have been several previous cladistic analyses of basal relationships in angiosperms (Young 1981; Dahlgren and Bremer 1985; Lammers *et al.* 1986). However, all these studies suffer from problems concerning the inclusion of taxa, aspects of character analysis (e.g. polarity assessment, treatment of multistate characters), and computer-assisted exploration of the data (for a detailed critique of Young's analysis, see Riggins and Farris 1983). As a result, phylogenetic conclusions were limited, and the resulting cladograms show little congruence. We have endeavoured to overcome these problems in the present analysis.

Methods

Taxa

Considering the wide range of ideas on relationships of Hamamelidae and the tremendous diversity of angiosperms as a whole, a definitive analysis of hamamelid relationships would have to include a prohibitively large number of taxa. In our experience with existing algorithms, it is difficult to be confident of finding most parsimonious trees when there are more than about 25–30 taxa, especially when character conflict is common, as it is in the present data set. This problem is compounded when one wishes to explore alternative trees. Choice of taxa therefore involved compromises. Our main priority was to include all taxa needed to resolve relationships at the base of the angiosperms and between magnoliids and the most primitive hamamelids, but our desire to keep the number of taxa within manageable limits led us to collapse many large groups whose monophyly and internal relationships should be tested in future analyses.

Our primary analysis involved the 27 taxa listed in Table 3.1. These include all dicot families with monosulcate and related pollen types (other than triaperturate), or Magnoliidae in the sense of Takhtajan (1987), except for the highly specialized and questionably related *Ceratophyllum*, Rafflesianae, and Nepenthanae. However, we performed a separate cladistic analysis of Laurales (to be presented elsewhere),

Table 3.1.   List of taxa and abbreviations.

Hypothetical ancestor	
(=ancestral states based on outgroup comparison)	ANC
Magnoliaceae	MAG
Winteraceae	WIN
Degeneria (=Degeneriaceae)	DEG
Eupomatia (=Eupomatiaceae)	EUP
Himantandraceae (=*Galbulimima*)	HIM
Annonaceae	ANN
Canellaceae	CAN
Myristicaceae	MYR
Austrobaileya (=Austrobaileyaceae)	AUS
Amborella (=Amborellaceae)	AMB
Trimeniaceae	TRI
Chloranthaceae	CHL
Calycanthaceae (including *Idiospermum*)	CAL
Monimiaceae *sensu lato*, Gomortegaceae,	
Hernandiaceae, Lauraceae	MON
Lactoris (=Lactoridaceae)	LAC
Saururaceae	SAU
Piperaceae	PIP
Aristolochiaceae	ARI
Nymphaeaceae (including *Barclaya*)	NYM
Cabombaceae	CAB
Nelumbo (=Nelumbonaceae)	NEL
Illicium (=Illiciaceae)	ILL
Schisandraceae	SCH
Ranunculidae (Takhtajan 1987)	RAN
Trochodendrales (=*Trochodendron, Tetracentron*)	TRO
Hamamelidales (=*Cercidiphyllum, Euptelea,*	
Platanus, Hamamelidaceae)	HAM
Liliopsida (=monocotyledons)	LIL

which indicated that *Hortonia*, Monimiaceae *sensu stricto*, Atherosperma-taceae, Siparunaceae, *Gomortega*, Hernandiaceae, and Lauraceae form a very robust clade that could be reduced to a single taxon (MON in the figures, or 'core Laurales'), united by stamen filaments, nectaries, and inaperturate pollen, and that Calycanthaceae and *Idiospermum* can also be lumped. The remaining groups are monocots (reduced to a single taxon) and six taxa with tricolpate pollen: *Illicium*, Schisandraceae, *Nelumbo*, Ranunculidae, Trochodendrales, and Hamamelidales (*Cercidi-phyllum, Euptelea, Platanus,* Hamamelidaceae). We did not include any exclusively fossil groups; many Cretaceous pollen and leaf types, such as *Afropollis, Eucalyptophyllum, Vitiphyllum,* and *Proteaephyllum reniforme,* may represent extinct families of primitive angiosperms, but these are known only as isolated organs, and with so much missing character information their positions would be highly unstable. However, in several cases fossils

did influence our scoring of taxa, and relationships between our results and the early angiosperm fossil record are discussed below.

At first sight, our concentration on primitive angiosperms may seem inappropriate, since primitive angiosperms alone constitute a paraphy-letic group, whereas in cladistic analysis the study group should be monophyletic. However, we emphasize that we regard this study not as an analysis of primitive angiosperms alone but rather of angiosperms as a whole, with certain taxa serving as 'placeholders' for much larger clades, on the assumption that they possess the basic states of these clades. In other words, 'higher' groups are implicitly included under the assumption that they are nested within (derived from) groups in the analysis, such that they are unlikely to exert a significant effect on estimates of relationships near the base of the angiosperms. Specifically, we assume that Hamamelidales are a placeholder for most remaining dicots (Rosidae, Dilleniidae, Asteridae, and possibly Caryophyllidae); this view is supported by some character data (e.g. secondary chemistry, floral symmetry, pollen: Kubitzki 1973; Ehrendorfer Vol. 40A, Ch. 1) and preliminary cladistic analyses (Donoghue 1987). Obviously, these are rather bold assumptions, which we fully intend to test by expanding the analysis to include additional groups. Nevertheless, the taxa included in this study illustrate much of the range of diversity in relevant characters and character combinations, and we therefore expect that the picture of relationships presented here will be fairly stable to the addition of taxa.

Characters

In amassing data, we tried to extract as many potentially informative characters as possible from the valuable compendium of Cronquist (1981) and the basic literature on the groups in question. For some taxa, we found surprisingly little information on rather basic characters, such as phyllotaxy (spiral *vs.* distichous) in Piperales. We excluded some characters because there was too much missing information or too much variation within taxa to be certain about scoring. Some of these may eventually prove useful as new data accumulate and relationships within taxa are resolved (e.g. ptyxis: Cullen 1978). We excluded autapomorphies and universal characters, since these provide no information on relationships among terminal taxa.

There are 54 characters in the resulting data set (see Appendix for a list of characters and the data matrix). Forty-two of these are binary characters and 12 are multistate characters; there are a minimum of 69 character state changes (steps) in the absence of homoplasy. In the case of multistate characters, the states were treated as unordered. This is a

conservative approach; more information on the ordering of states may allow better resolution in the future.

One frequently encountered problem concerned assessing the basic character states of terminal taxa when there was internal variation. In some cases we were able to score taxa based on previous cladistic work (e.g. we used our analysis of Laurales to reconstruct basal states of the core Laurales, and in several cases we referred to a preliminary cladistic analysis of Ranunculidae by Loconte and Estes, unpublished). In other cases we relied on less explicit ideas on relations within groups (e.g. in Annonaceae we assumed that taxa with monosulcate monad pollen are basal; in Aristolochiaceae, *Saruma*). In a few instances fossils were brought into the decision; for example, we scored Trochodendrales as having palmate venation, based on leaves that apparently represent primitive members of this group (Wolfe Vol. 40A, Ch. 5). When these approaches still left us uncertain, we scored taxa as unknown for the character. This was especially common in the case of monocots, where hypotheses on which groups are basal are so varied (cf. Dahlgren and Rasmussen 1983). We also scored some characters as unknown when we encountered major difficulties in the initial assessment of homology. For example, we were reluctant to score monocots for many leaf characters because of uncertainty over homology of the leaf as a whole.

Rooting was accomplished by a strict and conservative application of outgroup comparison, based on the results of our analysis of seed plants (Doyle and Donoghue 1986). According to this study (and Crane 1985), seed plants are a monophyletic group, originally of a 'seed fern' type, with coniferopsids and Mesozoic seed ferns derived from a common ancestor with platyspermic seeds and saccate pollen, like the Carboniferous seed fern *Callistophyton*. Angiosperms, Bennettitales, *Pentoxylon*, and Gnetales form a strongly supported group within the platyspermic clade, designated anthophytes because they all have flower-like strobili. Anthophytes are most parsimoniously united with *Caytonia*, based on reflexed cupules and seed structure, and in turn with other Mesozoic seed ferns. Within anthophytes, angiosperms are the sister group of the remaining groups. Thus, the first outgroup in the present analysis consisted of Bennettitales, *Pentoxylon*, and Gnetales, and the second outgroup was *Caytonia*. When one of the states of a character occurred in both outgroups, or when it occurred in one outgroup and the condition in the other was unknown, this state was assumed to be ancestral; when conditions in the two outgroups differed, the ancestral state was considered equivocal (Maddison *et al.* 1984). In this way we were able to polarize 30 characters; in effect, the resulting trees are rooted by these characters alone. The list of ancestral states, with equivocal characters scored as unknown, was entered in the analysis as a hypothetical ancestor; this procedure makes it possible to find globally most parsimonious ingroup cladograms (Maddison *et al.* 1984; Donoghue and Maddison 1986).

Analyses

All cladistic analyses were conducted using Wagner parsimony algorithms, which attempt to find the branching diagram that minimizes the total number of character state changes, allowing both forward and reverse changes. The data set was too large to make use of 'branch and bound' algorithms that guarantee finding all most parsimonious trees. In order to search for most parsimonious trees, we used PAUP (version 2.4, D. L. Swofford), run on an IBM PC AT, employing various combinations of options including local and global branch swapping, several methods of stepwise OTU addition (ADD-SEQ), and retention of multiple equally parsimonious trees (MUL-PARS). An analogous data set, in which we used the 'X-coding' method of Doyle and Donoghue (1986) to express partial ordering of multistate characters, was analysed with the METRO program in PHYLIP (version 3.0, J. Felsenstein); this was often useful in finding unanticipated, slightly less parsimonious topologies. Trees resulting from these analyses were input to MacClade (version 2.1, W. P. and D. R. Maddison) in order to calculate the parsimony of a wide variety of alternative topologies and to explore implications of topologies for character evolution; this actually led to the discovery of several additional most parsimonious trees. The cladograms shown here were generated using MacClade; where lines are shaded, this indicates the most parsimonious 'mapping' (optimization) of the states of a particular character on the cladogram. There may be several equally parsimonious ways to map character states on a tree (e.g. a state may arise twice or arise once and be reversed); in such cases (shown by horizontal hatching in MacClade), we will say that a state 'may be' homologous or 'may unite' particular taxa on the tree.

Results and discussion

Altogether, we have identified over 30 most parsimonious trees of 178 steps. This may not be an exhaustive inventory of most parsimonious trees, but all those found have the same general structure, and we suspect that any additional trees will be fairly similar. The overall consistency index is 0.39, which is somewhat below average for this number of taxa (Sanderson and Donoghue unpublished). This agrees with the traditional impression that homoplasy is widespread in primitive angiosperms.

To provide a point of reference, we begin by discussing one most parsimonious cladogram in some detail (Fig. 3.1), summarizing relationships of major groups and character support, with emphasis on the position of hamamelids and characters of special relevance to this question. Some differences among most parsimonious trees will be mentioned during description of this tree, while others deserving more attention will be discussed separately. A consensus tree is shown in Fig. 3.2.

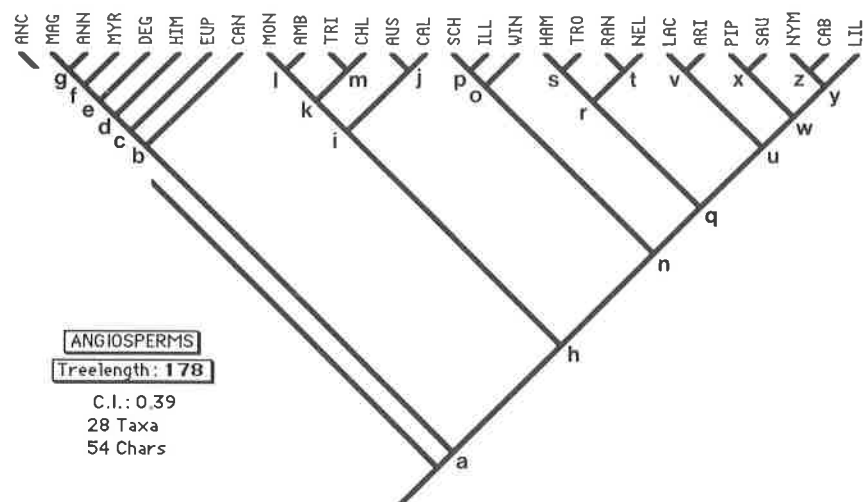One of the basal branches in Fig. 3.1 consists of seven families of the

ANGIOSPERMS
Treelength: 178
C.I.: 0.39
28 Taxa
54 Chars

Fig. 3.1. One most parsimonious cladogram requiring 178 character state changes (steps); see text for discussion. Character state changes associated with all internal nodes (designated by letters) and terminal taxa are presented below. A change to state 1 (from any other state) is indicated simply by the character number; in other cases, including reversals to 0, the derived state is given in parentheses after the character number. A question mark indicates that there are other equally parsimonious ways to map the character on the cladogram. **a**: 3, 30; **b**: 6, 24, 54?; **CAN**: 26, 46; **c**: 20(0)?, 28; **EUP**: 14, 15?, 23?, 39, 47, 54(2); **d**: 5, 9; **HIM**: 6(0), 23?, 40; **e**: 15?, 30(0), 45; **DEG**:14, 32(0)?, 38?; **f**: 8, 28(0), 42(0); **MYR**: 6(0), 21(0), 22(2), 26, 35, 38?, 40(2), 50; **g**: 12, 32(0)?; **MAG**: 14, 52(0); **ANN**: 4, 47, 54(0); **h**: 33, 37; **i**: 13, 15(2), 35; **j**: 17?, 28, 54(2)?; **AUS**: 45; **CAL**: 4, 6, 20(0)?, 32(0), 39, 42(3), 51(2); **k**: 19, 21(0), 36, 40, 44?, 52(0)?; **l**: 7, 13(2), 33(0), 42(2), 54?; **MON**: 12?, 27; **AMB**: 3(0), 15, 17?, 37(0), 41; **m**: 38; **TRI**: 20(0)?, 46; **CHL**: 21(2), 22(3), 34, 41; **n**: 44?, 52(0)?; **o**: 8, 20(0)?, 34?, 46, 54?; **WIN**: 3(0), 29; **p**: 13(2), 19?, 31, 48; **SCH**: —; **ILL**: 40(2), 42(0)?, 44(0); **q**: 16?, 17(2), 27, 42(0)?; **r**: 10(0), 19?, 31, 34?, 35; **s**: 21(2), 22(2); **HAM**: —; **TRO**: 3(0); **t**: 12, 20(2)?, 50; **RAN**: 16(0)?, 24, 46; **NEL**: 1, 2?, 3(2), 11, 18, 19(0)?, 32(0), 40, 42(3)?, 51(2), 53?; **u**: 20(2)?, 22, 24, 25; **v**: 4, 15?; **LAC**: 13, 22(2), 29, 37(0)?, 50; **ARI**: 34?, 39; **w**: 2, 54?; **x**: 14?, 15?, 20(3), 21(2), 22(3), 32(2), 41, 49, 51?; **PIP**: 40(2), 42(2); **SAU**: 35?; **y**: 1, 10(0), 30(0), 53?; **LIL**: 3(2)?, 14?, 37(0); **z**: 11?, 32(0), 33(0), 43, 46?, 51?; **NYM**: 3(0)?, 8, 22(0), 24(0), 25(0); **CAB**: 16(0), 18, 42(3).
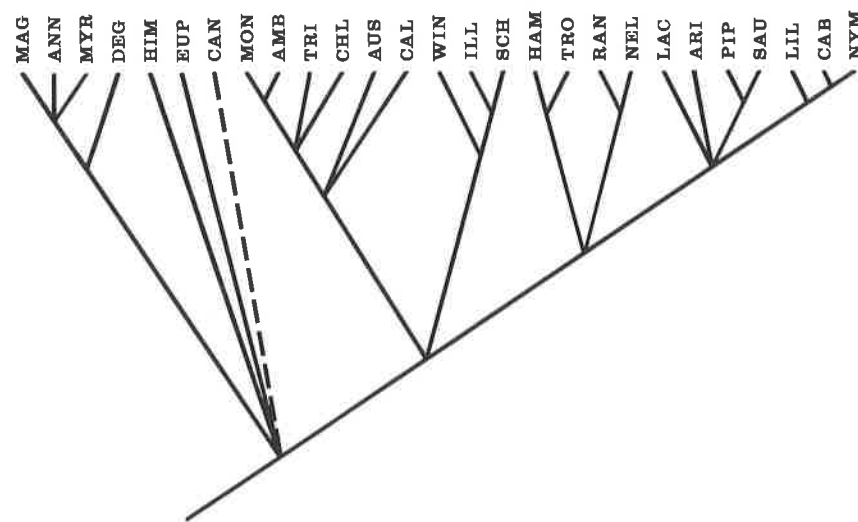
Fig. 3.2 A consensus of most parsimonious trees. This is a strict consensus tree, except that the alternative position of Canellaceae as sister group of Winteraceae and Illiciales is not indicated.

Magnoliales of Cronquist (1981), excluding Winteraceae, Austrobaileyaceae, and Lactoridaceae (which occupy near-basal positions in clades nested higher in the tree). These groups, which retain primitively granular monosulcate pollen (cf. Walker and Walker 1984), are united by trimerous perianth and PI-type sieve-tube plastids. For convenience, we will use the term 'Magnoliales' to refer to these seven taxa, even though they do not correspond exactly to Magnoliales in the sense of other authors and are not monophyletic in all trees. As discussed below, association of the basal members of this group (Canellaceae, *Eupomatia*, and Himantandraceae) is not secure. However, *Degeneria*, Myristicaceae, Annonaceae, and Magnoliaceae, or the 'core Magnoliales', form a more robust group, united by distichous phyllotaxy, boat-shaped pollen, and a sarcotesta or possibly derived aril. Himantandraceae may be associated with the core group on the basis of stratified phloem and septate pith.

The remaining angiosperms appear to form a monophyletic group, which we will term the 'columellate' clade because it is united primarily by two pollen characters, columellar infratectal structure and endexine. Exceptions, such as occurrences of granular structure in higher Laurales (associated with reduced, inaperturate pollen) and Nymphaeales, are most parsimoniously interpreted as reversals. Within this group there are three main clades, whose exact interrelationships are uncertain.

Thus, in Fig. 3.1 we show the second and third clades as united by non-multiplicative testa and non-ruminate endosperm, but it is not certain that these are synapomorphies: the testa may have become non-multiplicative in the common ancestor of columellates and then reversed in *Austrobaileya*–Calycanthaceae, and it is unclear whether ruminate endosperm is basic in angiosperms. Other characters potentially unite the first and third clades (sculptured pollen apertures, lack of a palisade exotesta), but these are also equivocal as synapomorphies. As all arrangements of the three clades are equally parsimonious, they are best regarded as forming an unresolved trichotomy, the resolution of which must await additional character data.

The first columellate clade corresponds to Laurales in a broad sense, with the notable inclusion of *Austrobaileya* and Chloranthaceae. This group is united by opposite leaves, unilacunar nodes, and sculptured pollen apertures (the spiral phyllotaxy of Lauraceae is most parsimoniously interpreted as a reversal). Within Laurales, Calycanthaceae and *Austrobaileya* are basal, and the remaining groups form a clade united by uniovulate carpels, chloranthoid teeth (apparently lost or transformed into monimioid teeth in advanced groups), and supratectal spinules. Chloranthaceae are linked with Trimeniaceae based on their unicarpellate flowers, which agrees with the view of Endress (1987); they are completely separated from Piperales where they are often placed (seven extra steps are needed to associate these two groups). *Amborella* is linked with the core Laurales on U-shaped sclereids, granular exine, and true drupes (in contrast to the one-seeded berries of other groups: Endress 1987).

The second columellate clade consists of Winteraceae and Illiciales (*Illicium*, Schisandraceae), united by coarsely reticulate, semitectate exine sculpture, as proposed by Walker and Walker (1984), plus branched sclereids and a palisade exotesta. Within this 'winteroid' clade, Illiciales are united by tricolpate pollen and unilacunar nodes.

The third columellate clade is united by palmately veined leaves and stamens with well-differentiated anthers and filaments. Two other possible synapomorphies are a shift to dehiscent fruits and the presence of stipules; we defined stipules adnate to the petiole as the derived state and scored other types (as in Trochodendrales and Hamamelidales) as unknown, because of their sporadic occurrence within terminal taxa and uncertain homology. In Fig. 3.1, this 'palmate' clade splits into two major lines, but other arrangements are equally parsimonious (see below). One line contains all the tricolpate groups except Illiciales. The other line, here called the 'paleoherbs', is characterized by anomocytic stomata, two perianth cycles, and trimery in both the perianth and the androecium (except for loss of one or both perianth cycles in *Lactoris* and Piperales and secondary multiplication of parts in Nymphaeaceae).

Arrangements within this clade are incompletely resolved. The *Lactoris*–Aristolochiaceae link is supported only by simple vessel perforations; it is not seen in all trees. In Fig. 3.1, Piperales are united with Nymphaeales (excluding *Nelumbo*) and monocots based on the loss of normal cambial activity, but in equally parsimonious trees Aristolochiaceae, *Lactoris*, and Piperales are united on distichous phyllotaxy. However, the link between Piperaceae and Saururaceae is very strongly supported (tetracytic stomata, spicate inflorescences, minute pollen, orthotropous ovules, sclerotic tegmen). Nymphaeales are united with monocots (as widely assumed) based on early replacement of the radicle by adventitious roots; another possible homology is lateral fusion of the cotyledons (Haines and Lye 1975), but we scored the monocotyledonous condition as unknown, to allow but not to assume homology.

The group of prime interest for our present purposes is the tricolpate clade, which contains the hamamelids. Besides tricolpate pollen, these taxa are united by loss of oil cells, sculptured pollen apertures, and possibly reticulate exine. Within this group, Ranunculidae are united with *Nelumbo* on the presence of benzylisoquinoline alkaloids, anomocytic stomata, nuclear endosperm, and possibly herbaceousness (for which ranunculids were scored unknown). Association of *Nelumbo* with Nymphaeales adds at least one step, despite similarities in vegetative morphology, pollen size, and seedling structure. Trochodendrales and Hamamelidales are united on spicate–racemose inflorescences and one perianth cycle. However, we emphasize that this does not mean that these two orders, or Hamamelidae as a whole, form a monophyletic group, since we assumed at the outset that Hamamelidales may be a placeholder for more derived groups. Our results are therefore consistent with the idea that lower Hamamelidae are relicts of an intermediate floral reduction phase in the evolution of Rosidae and other higher dicots, but they imply that this reduction was independent of that in Chloranthaceae and Piperales (contrary to Walker and Walker 1984).

Perhaps our most intriguing result is the inference that the first tricolpate dicots (except Illiciales) had palmate leaf venation. This was proposed for lower Hamamelidae by Hickey and Wolfe (1975), but they did not consider that the palmate venation of hamamelids might be homologous with that of herbaceous monosulcate groups, which they assumed originated independently three times. Since not all members of these groups are palmate, some explanation of our scoring may be in order. We scored Trochodendrales as palmate, although *Trochodendron* is pinnate, based on fossil relatives of *Trochodendron* with palmate venation (Wolfe Vol. 40A, Ch. 5), but we scored Hamamelidales as unknown because there are so many different conditions within them: palmate in *Cercidiphyllum*, pinnate but basally crowded in *Euptelea*, palmately lobed

in *Platanus* and some Hamamelidaceae (*Liquidambar*, *Exbucklandia*) but pinnate in others. We scored ranunculids as palmate based on Menispermaceae and the assumption that the ternate organization of other groups is more readily derived from palmate than from pinnate. If our results are correct, palmate venation should not be considered a synapomorphy of those hamamelid groups with this trait; instead, it is the plesiomorphic state. Many rosids and dilleniids have pinnate venation; if these groups are nested within hamamelids, our results imply that this condition is secondary. For Rosidae, one may envision a scenario involving dissection into a platanoid leaf and then a pinnately compound *Sapindopsis* type, followed by reversion to simple leaves in some groups. Clearly, further analyses, with the addition of many more groups, are necessary to test these possibilities.

Alternative basal relationships

Some of the most interesting variations among most parsimonious trees concern the arrangement of groups at the base of the tree—in particular, different positions of the root, which in turn reflect uncertainties in polarizing characters based on outgroup comparison. In Fig. 3.1, the seven taxa of Magnoliales form a basal clade. However, in other most parsimonious trees Himantandraceae are the sister group of all other angiosperms, or Canellaceae, *Eupomatia*, and Himantandraceae are variously associated with the columellate clade. In some (Figs 3.3A, B), Canellaceae are linked with Winteraceae and Illiciales, based on presence of a palisade exotesta (cf. Corner 1976). In other words, angiosperms may be rooted within the Magnoliales, which would then be paraphyletic.

These different rooting arrangements have many different implications for early angiosperm evolution. For example, in Fig. 3.1 (with Magnoliales forming a basal clade), PI sieve-tube plastids and trimerous perianth unite the Magnoliales and originate only once or twice elsewhere, but in Fig. 3.3A (with Magnoliales paraphyletic), both features arise in a more scattered fashion. In addition, the various schemes often provide different estimates of primitive states for characters that we were unable to polarize using outgroup comparison. In Fig. 3.1, inner staminodes, stratified phloem, and septate pith arise within Magnoliales, but in Fig. 3.3B, these traits are or may be primitive in angiosperms. For these characters, Fig. 3.1 agrees better with conventional views. However, this tree implies that the boat-shaped pollen of core Magnoliales is a reversal, not primitive as widely assumed; it is primitive only if Magnoliales are paraphyletic. These results suggest that revision of conventional assumptions on one or more of these characters is in order.
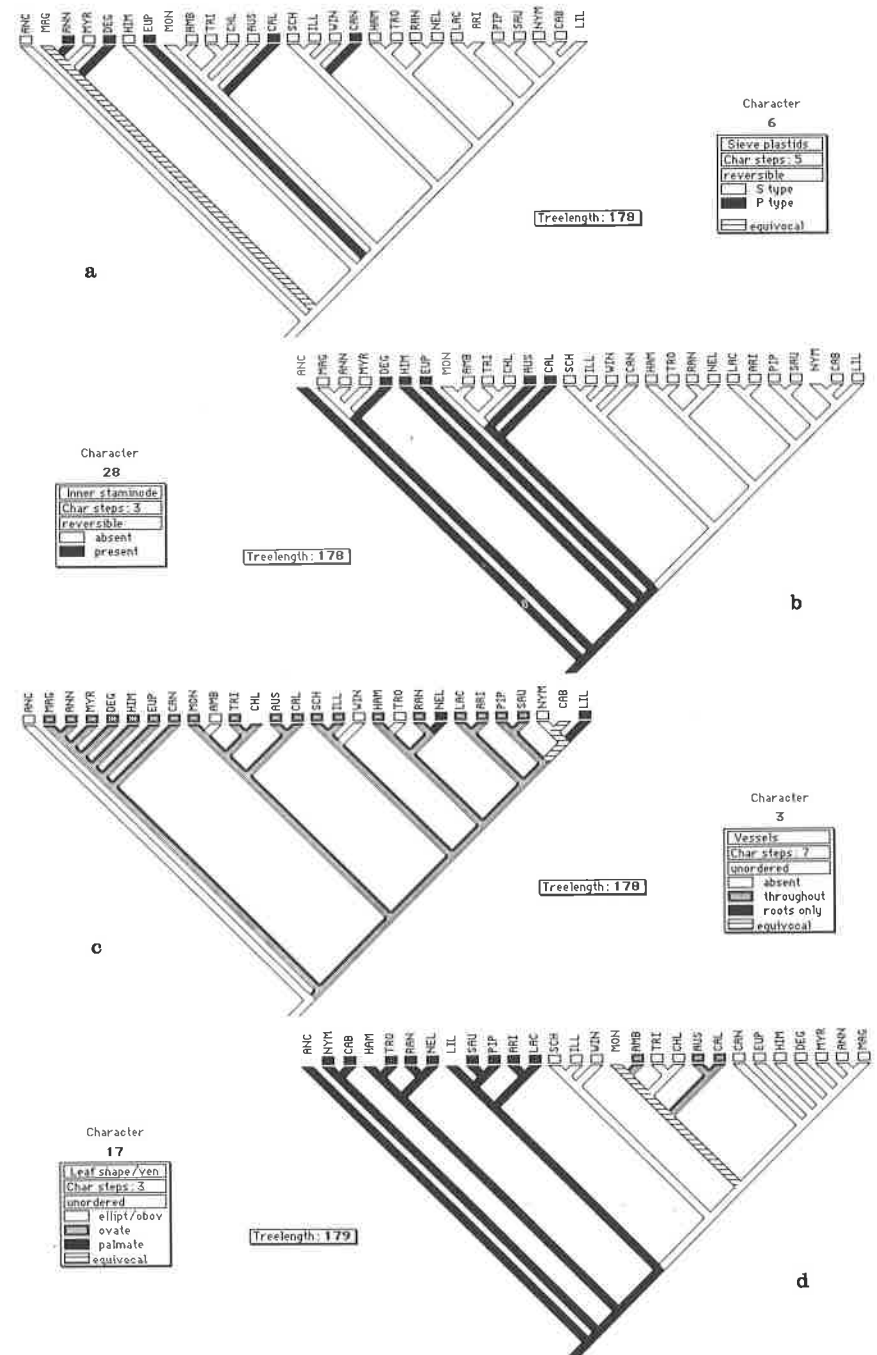
Fig. 3.3 Alternative arrangements at the base of the angiosperms, with implications for character evolution shown by shading. Boxes below names of taxa indicate character states (blanks = state scored as unknown). (A) 'Magnoliales' paraphyletic, showing the sieve-tube plastid character; (B) same tree, showing the inner staminode character; (C) Magnoliales monophyletic (Fig. 3.1), showing the vessel character; (D) Nymphaeales basal, showing the leaf shape/venation character.

All of our most parsimonious trees conflict with traditional views on vessel evolution (Fig. 3.3C). We coded vessels as primitively absent, based on outgroup comparison: although we assumed that Gnetales are related to angiosperms, vessels are presumably not homologous in the two groups, since Gnetales are nested among vesselless Bennettitales and *Pentoxylon* (Doyle and Donoghue 1986). Nevertheless, it is most parsimonious to assume that vessels originated at the very base of the tree and were subsequently lost in Winteraceae, *Amborella*, Trochodendrales, and Nymphaeales (another supposed vesselless group, *Sarcandra* in the Chloranthaceae, actually has vessels in the roots: Carlquist 1987). This conclusion was also reached by Young (1981), but we believe that it is now on more solid ground. Many will object to this result, on the grounds that there is no situation in which loss of vessels would be advantageous for a land plant. Three additional steps (eight origins) are required to assume that evolution of vessels was irreversible; this is not an overwhelming parsimony debt, but it does imply that the functional arguments for such an assumption should be scrutinized. We suggest that it is not inconceivable on functional grounds that vessels were lost in primitive angiosperms. First, what is implied is the loss of very primitive vessels, not specialized ones. In early vesseliferous angiosperms, other cell types and organs were presumably less dependent upon the presence of vessels (i.e. vessels were less 'burdened': Riedl 1978), and their loss might therefore be less deleterious than in advanced forms. Furthermore, Carlquist (1975) has argued that vessels are less vital in environments such as wet tropical uplands, where most vesselless angiosperms occur today. He interprets these as the only habitats where vesselless forms could survive, but one might also argue that these are the habitats where loss of vessels would have the least negative effect. Finally, there may be situations where vesselless wood is superior: for example, where freezing results in air embolisms. Here it may be relevant that one vesselless group, Trochodendrales, was abundant at high latitudes during the Late Cretaceous and early Tertiary (Wolfe Vol. 40A, Ch. 5).

We also experimented with several alternative positions of the root. For example, we found trees with Nymphaeales basal, then tricolpates, then other paleoherbs (including monocots) that are only one step longer than our best trees (Fig. 3.3D). This topology implies that the first angiosperms had palmate venation, anomocytic stomata, distinct filaments, and endexine; these traits are usually considered derived, but we were unable to polarize them on strict outgroup comparison. Trees rooted among the paleoherbs, with Nymphaeales plus monocots forming a basal clade, are only slightly worse (181 steps). However, trees rooted next to Chloranthaceae (cf. Burger 1977), which would be consistent with the prevalence of chloranthoid pollen, leaves, and

flowers in the Early Cretaceous (Upchurch 1984; Walker and Walker 1984; Friis *et al.* 1986), are much worse (185 steps). Because Chloranthaceae share several features with Gnetales (opposite leaves, two-trace nodes, orthotropous ovules), these trees would be improved if angiosperms were linked directly with Gnetales (cf. Crane 1985). However, this arrangement is less parsimonious than one with the angiosperms basal in the anthophytes (Doyle and Donoghue 1986).

Alternative relationships within the columellate clade

In addition to the three equally parsimonious arrangements of Laurales, winteroids, and palmates, there are several equally parsimonious arrangements within the palmate clade. Most importantly, the ranunculid clade can be dissociated from the hamamelids and united directly with the paleoherbs on the basis of herbaceous habit and anomocytic stomata (Fig. 3.4A). This topology implies that tricolpate pollen originated three times (or originated twice and was lost at the base of the paleoherbs), and that oil cells were lost below the hamamelid branch and regained in Aristolochiaceae, *Lactoris*, and Piperales. Both might be seen as reasons to consider this arrangement less plausible than Fig. 3.1.

This observation led us to ask how much worse it would be to assume that tricolpate pollen evolved only once. The most parsimonious arrangement that allows this possibility unites the hamamelid–ranunculid clade with Illiciales, within the winteroid clade (Fig. 3.4B). Here, the tricolpate groups are united by both tricolpate pollen and chloranthoid teeth, and are linked with Winteraceae on reticulate exine sculpture. This topology adds only two steps overall. However, there are morphological reasons to suspect an independent origin of tricolpate pollen in Illiciales: in *Illicium* the colpi are unusually long, and in Schisandraceae they are fused at one pole and have a peculiar median ridge (Walker 1976a).

Along similar lines, we explored the possibility that chloranthoid teeth are homologous in all groups in which they occur. With our shortest trees, it is most parsimonious to assume that chloranthoid teeth arose independently at least three times: within Laurales, in Illiciales, and in the tricolpate (ranunculid–hamamelid) clade (Fig. 3.4C). However, on these trees only one extra step is required to assume that teeth arose once in the common ancestor of the whole columellate clade and were lost (four times) in derived groups lacking teeth. Considering alternative topologies, we found that uniting tricolpates directly with Chloranthaceae, as suggested by Hickey and Wolfe (1975), adds at least four steps, due to reversals of lauralean advances. Because chloranthoid teeth also occur in Trimeniaceae and *Amborella*, they can be homologous
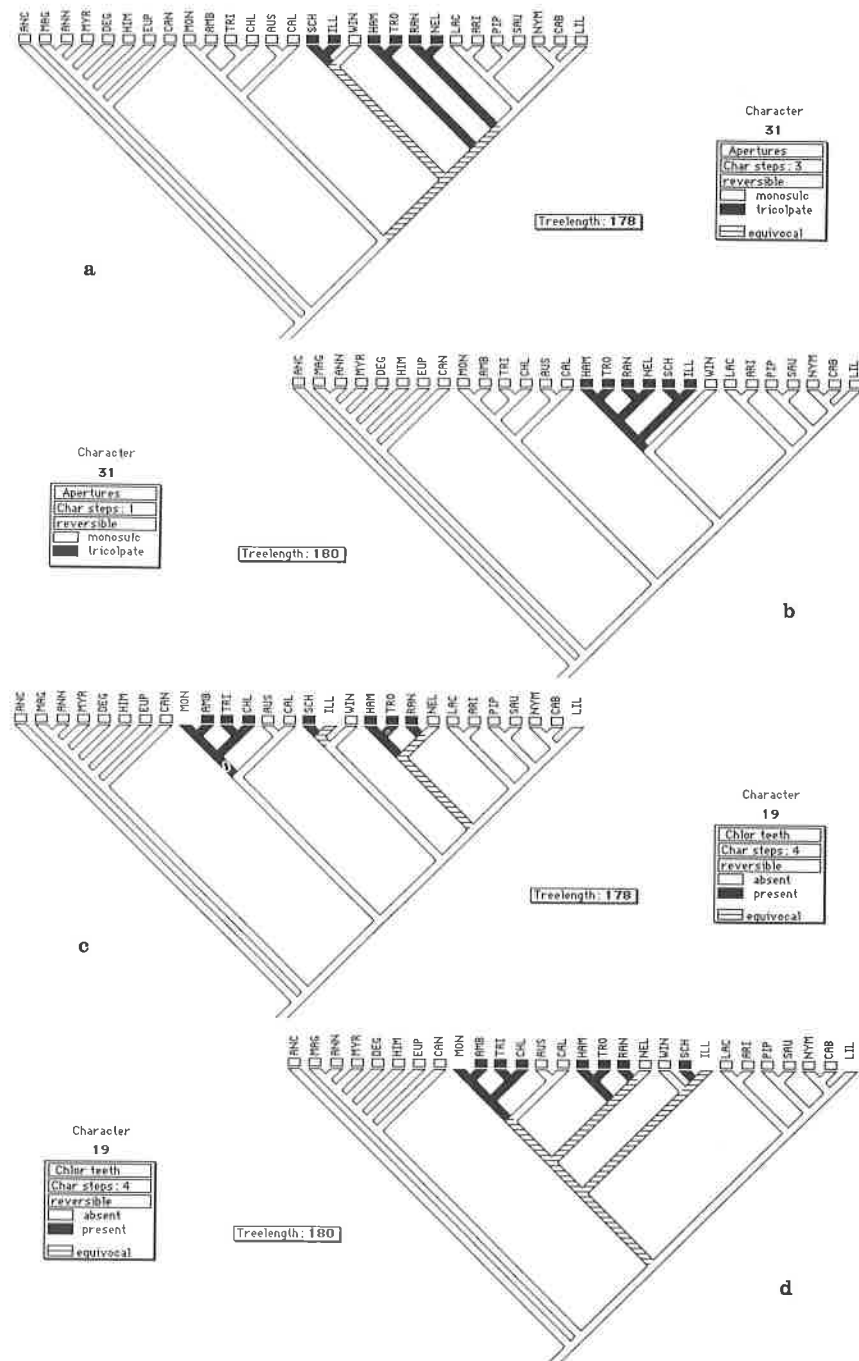
in tricolpates and Laurales if these two clades are considered sister groups (a relationship supported by sculptured pollen apertures). Some such trees are just one step longer than our best trees (179 steps), but in these teeth must arise independently in Illiciales. Trees in which winteroids, Laurales, and tricolpates all form a clade, which do permit a single origin (plus three losses) of chloranthoid teeth, are only two steps longer than our best trees (Fig. 3.4D). These observations suggest that it would be premature to rule out a single origin of chloranthoid teeth, or a relationship of the tricolpate groups to Laurales rather than to paleoherbs.

Relations to fossil evidence

Although we did not include any fossil groups in our analysis and only occasionally consulted fossils in assessing basic states within terminal taxa, our results show interesting relations to the Cretaceous angiosperm record, and we see several instances in which fossils might help resolve problems.

Probable members of all of our major angiosperm clades can be recognized in the Early Cretaceous, all relatively primitive in morphology. In the Aptian, Magnoliales appear to be represented by large, granular, monosulcate pollen (Ward *et al.* 1988); winteroids by ulcerate tetrads (Walker *et al.* 1983) and zonasulculates with similar sculpture (*Afropollis*, '*Retimonocolpites*' *mawhoubensis*: Doyle *et al.* 1988); Laurales similar to Chloranthaceae by *Clavatipollenites* (Walker and Walker 1984); and monocots by *Acaciaephyllum* leaves and *Liliacidites* pollen (Doyle 1973; Walker and Walker 1984). Various Aptian leaves may represent Magnoliales, winteroids, or Laurales (Wolfe *et al.* 1975; Hickey and Doyle 1977; Upchurch 1984). The tricolpate clade is first clearly represented by early Aptian pollen and mid-Albian platanoid and *Sapindopsis* leaves (Doyle *et al.* 1977; Hickey and Doyle 1977; Crane *et al.* 1986). Most interesting for our purposes, though, are Albian actinodromous leaves with cordate or peltate bases, and Aptian reniform leaves with crowded secondaries, which have been variously compared with Nymphaeaceae, *Nelumbo*, Menispermaceae, and *Cercidiphyllum* (cf. Hickey and Doyle 1977). Even if these leaves remain unassignable to modern families, our results suggest that they may belong to a single natural group, the tricolpate–paleoherb clade. Further study of their morphology (especially stomata, which are mostly laterocytic in lower Hamamelidae but anomocytic in Ranunculidae and paleoherbs), or their association with flowers or pollen, might provide character combinations that would help resolve relations among hamamelids, ranunculids, and paleoherbs.

Fossils may also provide critical evidence by clarifying basic pollen features in the tricolpate clade. In Fig. 3.1, sculptured apertures unite

Fig. 3.4   Alternative relationships within the 'columellate' clade, with implications for character evolution (cf. Fig. 3.3). (A) Ranunculidae linked with paleoherbs, showing the pollen aperture character; (B) tricolpate clade (hamamelids and ranunculids) linked with Illiciales, showing the pollen aperture character; (C) cladogram in Fig. 3.1, showing the chloranthoid tooth character; (D) winteroids, tricolpates, and Laurales forming a clade, showing the chloranthoid tooth character.

the four tricolpate groups but arise independently in Laurales; this character is more consistent with the almost equally parsimonious alternative relationship between tricolpates and Laurales (Fig. 3.4D). Another trait that might seem to favour lauralean affinities is supratectal spinules, seen in both Chloranthaceae and some lower Hamamelidae (Walker 1976b); however, this may not be basic in either Laurales or tricolpates, since it is absent in *Austrobaileya*, Calycanthaceae, Trochodendrales (Endress 1986b), and *Nelumbo*, and sporadic in Hamamelidales and Ranunculidae. The oldest known tricolpates, from the early Aptian of Gabon (Doyle *et al.* 1977; Doyle and Ward in preparation), suggest that both of these similarities to Laurales are misleading. These fossils have narrow colpi (usually irregularly spaced and slightly oblique in orientation) that lack pronounced sculpture, and smooth muri; both sculptured colpi and supratectal spinules appear only later in the Albian radiation of tricolpates. If these grains are related to modern tricolpates (as suggested by transitional forms in the Aptian–Albian), and if they illustrate the primitive condition in tricolpates (as the irregular colpi might imply), they suggest that the tricolpate clade was actually derived from ancestors with smooth muri and non-sculptured apertures, like most living paleoherbs, and that sculptured colpi arose within the group.

Another connection between our results and fossil evidence concerns the ecological radiation of early angiosperms. Association of the hamamelid clade with Ranunculidae and paleoherbs (as in Fig. 3.1) raises the possibility that its early members were more herbaceous than most modern Hamamelidae. This might fit sedimentological evidence that Aptian–Albian angiosperms (including tricolpate platanoids and *Sapindopsis*) tended to occupy disturbed habitats, such as stream margins (Hickey and Doyle 1977). Hickey and Doyle saw this as evidence that such ecology was primitive in angiosperms (Stebbins 1974), but it may apply principally to the palmate clade. This habit might help explain the rapid spread of tricolpates and paleoherbs in the Aptian–Albian and the fact that most modern angiosperms belong to these clades. The most important exception to the early dominance of palmates is the Chloranthaceae (judging from the abundance of *Clavatipollenites*); perhaps significantly, modern Chloranthaceae differ from most other Laurales in being weedy and semiherbaceous. The spread of tricolpates (and Chloranthaceae) from tropical habitats (Brenner 1976; Doyle *et al.* 1982) might help explain the trend for reversion to wind pollination within these groups (cf. Walker and Walker 1984).

Conclusions

Despite the preliminary nature of this study, some relationships at the base of the angiosperms already seem rather well supported (Fig. 3.2),

and we can identify hypotheses and characters that deserve more attention in the future. Thus it is uncertain, based on our conservative outgroup analysis, whether Magnoliales form a monophyletic basal line or a paraphyletic grade (as implied by many conventional views). However, Winteraceae (plus Illiciales), which are often included in Magnoliales, seem well nested within a clade with basically columellar exine structure that includes the bulk of the angiosperms. Our results confirm the unity of the Laurales, including Chloranthaceae, which seem to be quite unrelated to Piperales. An unexpected but apparently robust grouping is the paleoherb clade, including not only monocots and Nymphaeales but also Piperales, *Lactoris*, and Aristolochiaceae. Most surprising is the conclusion that Hamamelidae and other tricolpate taxa (except Illiciales) may be related to the paleoherbs, based on palmate leaf venation and differentiated stamens. However, trees linking tricolpates and Laurales (though not specifically Chloranthaceae), which would permit the homology of chloranthoid teeth, or linking tricolpates, Illiciales, and Winteraceae, which would permit a single origin of tricolpate pollen, are nearly as parsimonious and should be considered viable alternatives.

Although we have not considered relationships among hamamelids, our results have definite implications for future studies of this issue, and of the relationships of 'higher dicots' in general. Since 'lower hamamelids' are very likely paraphyletic, they must be split up into component monophyletic groups to allow the possibility that other groups are nested among them, and possibly derived groups should be added to the analysis, perhaps initially in the form of reconstructed primitive rosids, dilleniids, and caryophyllids. To address the origin of 'higher hamamelids', still more rosid and dilleniid groups would have to be added. For practical reasons, these additions would require reducing the number of monosulcate groups. One approach would be to use our most parsimonious results to polarize characters in hamamelids and their presumed relatives. The most probable first outgroup of these groups is either Ranunculidae (including *Nelumbo*) or Ranunculidae plus paleoherbs; in either case ranunculids would play a key role in determining polarities. Beyond this, the paleoherbs should be consulted, especially the most plesiomorphic groups—*Lactoris*, Aristolochiaceae, and Saururaceae. Next most important are either Winteraceae–Illiciales or Laurales. It is probably unnecessary to consider Magnoliales or Chloranthaceae, since these are 'screened off' from having a substantial effect on polarity by more closely related taxa. A more conservative approach, in view of the almost equally parsimonious relationship between tricolpates and Laurales or Winteraceae, and the possibility that 'higher' groups might (contrary to our assumption) alter the best position of tricolpates, would be to retain more monosulcate groups in the analysis to allow a better evaluation of the global parsimony of

ingroup cladograms (Maddison *et al.* 1984). Here our results are helpful in indicating how the number of taxa can be reduced by condensing especially robust clades, such as core Magnoliales, 'higher' Laurales, Illiciales, Piperales, and Nymphaeales.

Acknowledgements

Appendix

Characters and character states

Polarized characters are indicated by (P), unpolarized by (U). All multistate characters are treated as unordered. Where not otherwise specified, data are from Cronquist (1981), supplemented as follows: anatomical characters (2–11, 13–14): Metcalfe and Chalk (1957, 1979), Metcalfe (1987); pollen characters (29–37): Erdtman (1952), Walker (1976*a,b*), Walker and Walker (1981, 1983) for Myristicaceae, Endress and Honegger (1980) for *Austrobaileya*; seed characters (43–49): Corner (1976), Endress (1980) for *Austrobaileya*, Endress and Sampson (1983) for Trimeniaceae, Endress (1987) for Chloranthaceae.

1. (P) 0 = radicle persistent; 1 = replaced by adventitious roots. Nymphaeales, *Nelumbo*: Corner (1976), Dahlgren *et al.* (1985); Piperales: Holm (1926), Vogel (1980).

2. (P) 0 = woody; 1 = herbaceous. Interfascicular cambium not producing normal vascular tissue scored as unknown (Esau 1953; Balfour 1958).

3. (P) 0 = vessels absent; 1 = present throughout; 2 = in roots only. Chloranthaceae: Carlquist (1987).

4. (P) 0 = perforations (or end-wall pitting) scalariform; 1 = simple. Taxa in which the most primitive condition is mixed scored as unknown.

5. (U) 0 = secondary phloem not stratified; 1 = stratified.

6. (P) 0 = sieve-tube plastids S type; 1 = PI type. Behnke (1981), Behnke and Barthlott (1983). PII type (monocots) scored as unknown to allow derivation from either state.

7. (U) 0 = U-shaped sclereids in pericycle absent; 1 = present.

8. (U) 0 = branched sclereids in leaves absent; 1 = present.

9. (U) 0 = pith without sclerenchymatous septa; 1 = with septa. Winteraceae: Metcalfe (1987) describes only scattered, sometimes grouped sclereids.

10. (U) 0 = oil cells absent; 1 = present.

11. (P) 0 = laticifers absent; 1 = present.

12. (P) 0 = benzylisoquinoline alkaloids absent; 1 = present. Hegnauer (1964–1973), Rezende *et al.* (1975), Gershenzon and Mabry (1983), Dahlgren and Bremer (1985). Taxa in which these alkaloids are generally lacking but have been reported are scored as unknown.

13. (U) 0 = nodes tri- or multilacunar; 1 = unilacunar, one-trace or with arc of several traces; 2 = unilacunar, two-trace.

14. (U) 0 = nodes uni- or trilacunar; 1 = multilacunar. Piperales: Holm (1926), Balfour (1958), S. Tucker (personal communication); Nymphaeaceae: Weidlich (1976); Cabombaceae: Moseley *et al.* (1984).

15. (P) 0 = phyllotaxy helical; 1 = distichous on at least some branches; 2 = opposite. Beck *et al.* (1982), Halle *et al.* (1978); *Lactoris*: S. Carlquist (personal communication); Saururaceae: S. Tucker (personal communication); Nymphaeaceae: Weidlich (1976).

16. (P) 0 = adnate/axillary stipules absent; 1 = present. Other stipule types scored as unknown (see text).

17. (U) 0 = leaves elliptical or obovate, secondary veins at constant angle or lower angle at base; 1 = ovate, basal secondaries crowded, at higher angle; 2 = actino- or acrodromous (palmate). Hickey and Wolfe (1975); JAD, personal observations.

18. (P) 0 = leaf base not peltate; 1 = peltate.

19. (P) 0 = chloranthoid teeth absent; 1 = present. See text. *Illicium* scored as unknown because teeth are present in *I. anisatum* but not in other species (Hickey and Wolfe, 1975).

20. (U) 0 = stomata mostly paracytic (> 90% of those on leaf); 1 = laterocytic or variable; 2 = anomocytic; 3 = tetracytic. Upchurch (1984; personal communication).

21. (U) 0 = cymose inflorescences; 1 = solitary flowers (occasionally 2–3); 2 = spikes or racemes. Trochodendrales, Hamamelidales: Endress (1986*b*, 1987).

22. (U) 0 = perianth with more than two whorls (spiral); 1 = two whorls; 2 = one whorl; 3 = absent. Himantandraceae, *Eupomatia* scored as unknown because of uncertain homology (Endress 1977); Trochodendrales: Endress (1986*b*).

23. (P) 0 = calyptra absent; 1 = present. Magnoliaceae, Winteraceae scored as unknown because of possible but uncertain homology (Endress 1977).

24. (P) 0 = perianth not trimerous; 1 = at least calyx trimerous. Endress (1986*a*), Kubitzki (1987). Taxa with some pentamerous members assumed to be basically trimerous.

25. (P) 0 = stamens not in threes; 1 = in multiples of three.

26. (P) 0 = stamens free; 1 = connate into a tube. Chloranthaceae: based on Albian flower of Friis *et al.* (1986); Schisandraceae: spiral mass questionably homologous with tube.

27. (U) 0 = stamens laminar; 1 = well-differentiated filament. Intermediate and excessively variable conditions scored as unknown. Aristolochiaceae based on *Saruma* (Dahlgren *et al.* 1985).

28. (U) 0 = inner staminodes absent; 1 = present.

29. (P) 0 = pollen shed as single grains; 1 = permanent tetrads.

30. (P) 0 = pollen boat-shaped; 1 = globose.

31. (P) 0 = monosulcate or derived inaperturate, zonate, etc.; 1 = tricolpate.

32. (P) 0 = pollen size large (>50 um); 1 = medium (ancestral state); 2 = small (<20 um).

33. (P) 0 = infratectal structure granular (including atectate); 1 = columellar.

34. (P) 0 = tectum continuous or finely perforate (foveolate); 1 = semitectate–reticulate.

35. (P) 0 = aperture membrane not conspicuously sculptured; 1 = sculptured.

36. (P) 0 = supratectal spinules absent; 1 = present.

37. (P) 0 = endexine absent in extra-apertural areas; 1 = present. Winteraceae: Roland (1971).

38. (P) 0 = carpels several-many; 1 = one (rarely 2).

39. (P) 0 = hypanthium absent; 1 = present.

40. (U) 0 = ovules several; 1 = one apical; 2 = one basal.

41. (U) 0 = ovules anatropous; 1 = orthotropous. *Amborella*: Endress (1987; personal communication).

42. (U) 0 = fruit dehiscent; 1 = berry; 2 = drupe (with endocarp); 3 = dry indehiscent. Laurales, Piperales: Endress (1987).

43. (P) 0 = seed not operculate; 1 = operculate.

44. (P) 0 = testa multiplicative; 1 = non-multiplicative. Where not characterized by Corner (1976), we adopted a limit of seven cells thick.

45. (U) 0 = sarcotesta absent; 1 = present. True arils scored as unknown to allow possible homology.

46. (U) 0 = palisade exotesta absent; 1 = present.

47. (U) 0 = fibrous mesotesta absent; 1 = present.

48. (U) 0 = sclerotic mesotesta absent; 1 = present.

49. (U) 0 = sclerotic (endo)tegmen absent; 1 = present.

50. (U) 0 = endosperm cellular; 1 = nuclear.

51. (U) 0 = endosperm only; 1 = perisperm plus endosperm; 2 = neither.

52. (U) 0 = endosperm not ruminate; 1 = ruminate. Himantandraceae: Endress (personal communication).

53. (P) 0 = cotyledons free; 1 = laterally fused. Haines and Lye (1975).

54. (P) 0 = chromosome number (n) 6–8; 1 = 12–19; 2 = 10–11. Raven (1975), Ehrendorfer (1976). Higher numbers scored as unknown because of ambiguous derivation.

Data matrix

	1	2	3	4	5
ANC	0000?0????	00??00?00?	00???0000?	?0000 10000	000???00???????00
MAG	00101?0111	0101?? 0000	10??000000	00000000000	0001000000001
WIN	0000000 1?	10?0000000	0?0?00000	1 1011 1001	0000?0 101000?0001
DEG	0010110011	00011000001	00100010001	000000000100	0100100000 101
EUP	0010010001	0?0 1100000	1?1?00010	101000000010	0100001000?0102
HIM	001?10001	10000000000	1?1?00010	101000 0?00	10 10?0?000?0101
ANN	0011110111	0100100000	?00100000	000?000000	00?0 10000100
CAN	0010010001	0?0000000	1?001?1?	0010 1?000000	00 10?0 1000?0?01
MYR	0010100111	0000100000	0201010	1?00001??	1?0 1020000??000 10101
AUS	0010000001	00102?1001	10000001	01011010	10000 100100?0?010?
AMB	0000001000	?0?20 10101	10000000	001010 0?100	?100?1120100000?0001
TRI	00100000?	10010200010	00000000010	11011 1101	01010101000?0000
CHL	0??0?000?1	0?102?0011	230???000	1011111?10	11 10?0000000000
CAL	001101?00	10010201000	100000010	10010?010	1003000000002?02
MON	00100?1001	012020?0??	000000 1?0	10100?110	?1020?0000000001
LAC	0011000001	0?101120022	01102?01	101?00?0000000	100000 1000?
SAU	0110?0000	10001112003	230?10100	102 10101000	100100000 101001
PIP	0?1??0000	10?01?1200	3230?1010	0102?0???	002120100001?1001
ARI	??110??00	10?001?2002	?10110100	1011 1?0?01	000010000000?00
NYM	1100?00100	10000120021	00000??000	00000100000	11010000?1011
CAB	11?0?00000	1??0?02102	110110100	0000000?	100003110100001 0?1
NEL	1120?00000	11???1210	210000010	01101110100	1030100000 12?10
ILL	0010000101	00200000?0	100000000	1111100?0	0200000101000001
SCH	0010?0010	10020000010	10000?000	11111001	000010101010 1000001
RAN	0?10?0?0000	10?002012?0	01?0?0011	11?1?100	00?0?01000100?0
TRO	000000??00	0000?0?201	12200001	0011110	10000001000 0?0000?
HAM	0010000?0	00000?0??0	11220000	1001111?	1?1000000 1000?0?000?
LIL	1120??00000	?001???????	101101000	011 1?0000000?0???	000?00??

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