Early Evolution of Flowers

Chapter · January 1994

DOI: 10.1007/978-3-7091-6910-0_2

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Pl. Syst. Evol. [Suppl.] 8: 7–29 (1994)

Origin of the angiosperm flower: a phylogenetic perspective

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Received February 21, 1994

Key words: Angiosperms, anthophytes, *Gnetales*, *Bennettitales*. – Flower, carpel, phylogeny, cladistics.

Abstract: Morphological and molecular analyses agree that angiosperms are monophyletic and somehow related to *Gnetales*, but uncertainties on rooting (among woody magnoliids or paleoherbs) and the position of fossils permit varied scenarios for origin of the flower. Trees linking angiosperms with *Bennettitales*, *Pentoxylon*, and *Gnetales* and this "anthophyte" clade with *Caytonia* imply that flowers arose in the common ancestor of anthophytes and carpels are cupule-bearing sporophylls. However, trees linking angiosperms with *Caytonia* and/or glossopterids imply that flowers originated more than once, as may certain fossil anthophytes. Trees linking anthophytes with coniferopsids suggest that flowers evolved by aggregation of fertile shoots into pseudanthia. New data on fossils or the control of floral morphogenesis in angiosperms and *Gnetales* might distinguish among these hypotheses.

Phylogenetic analyses of fossil and modern seed plants based on several morphological and molecular data sets have strengthened the hypothesis that angiosperms are monophyletic and revived the concept that their closest living relatives are the *Gnetales*. However, these analyses have given inconsistent results concerning relationships of angiosperms and *Gnetales* with fossil groups and basal relationships within angiosperms, and these lead to very different scenarios for the origin of the angiosperm flower. These conflicts are due partly to different assumptions on homologies and partly to the inclusion of different taxa, but experimental analyses show that many of the same alternatives are almost equally parsimonious even with one data set. Rather than defend one preferred scheme, it may therefore be more profitable to explore several of the most parsimonious alternatives and consider what sorts of new data might help to decide among them. To do so, I will concentrate on a data set designed to overcome weaknesses of previous studies, which dealt separately with relationships within angiosperms and between angiosperms and other seed plants, and to explore apparent conflicts between analyses based on morphological and rRNA data (DOYLE & al. 1994).

Previous euanthial scenarios

The first comprehensive phylogenetic analyses of seed plants by Crane (1985) and Doyle & Donoghue (1986, 1992) yielded generally consistent trees. Angiosperms were linked with Mesozoic *Bennettitales*, *Pentoxylon*, and living *Gnetales*, together called anthophytes because they all have flower-like reproductive structures, and this group was linked with so-called Mesozoic seed ferns. This result implies that the flower, in the sense of a short, specialized axis bearing closely aggregated sporophylls, rather than an unspecialized axis or an elongate strobilus, originated before the carpel. In Crane (1985) anthophytes were linked with Triassic corystosperms and angiosperms were nested within anthophytes, related directly to *Gnetales*, whereas in Doyle & Donoghue (1986, 1992) anthophytes were linked with the primarily Jurassic genus *Caytonia* and angiosperms were the sister group of other anthophytes (Fig. 1).

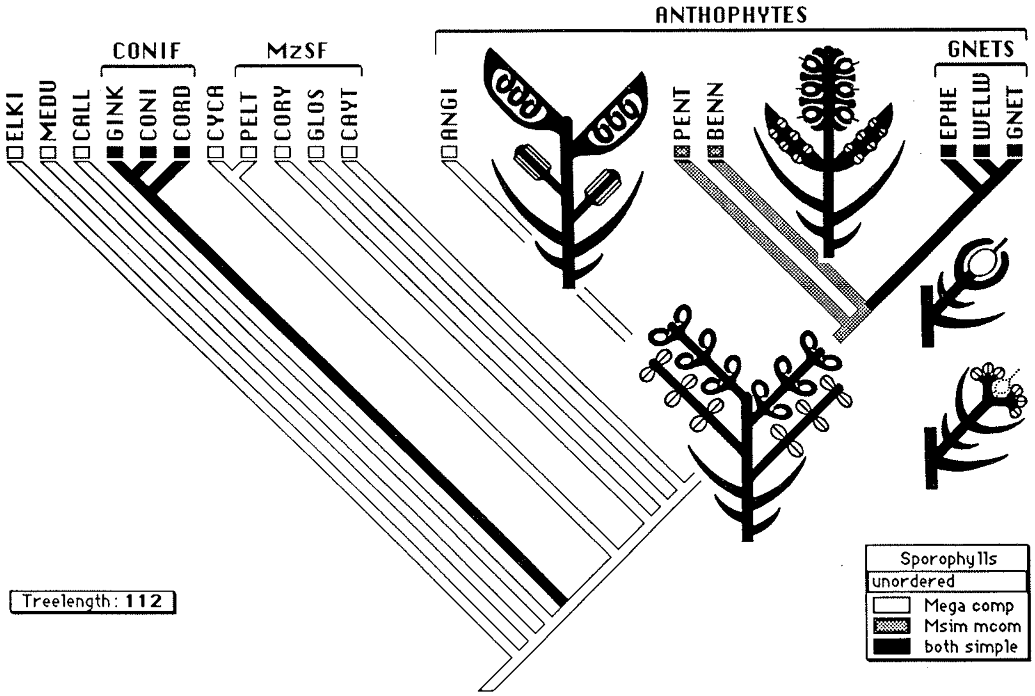


Fig. 1. Representative most parsimonious seed plant tree of Doyle & Donoghue (1992), showing distribution of the sporophyll character (both micro- and megasporophylls pinnately organized, microsporophylls pinnately organized but megasporophylls simple, both micro- and megasporophylls simple). Sketches summarize the morphology of the reproductive structures in angiosperms, *Bennettitales*, *Gnetales*, and the hypothetical common ancestor of anthophytes. ELKI *Elkinsia* (=Devonian "seed fern" in Doyle & Donoghue 1992), MEDU *Medullosaceae*, CALL *Callistophyton*, GINK *Ginkgoales*, CONI *Coniferales*, CORD *Cordaitales*, CYCA *Cycadales*, PELT *Peltaspermum*, CORY *Corystospermaceae*, GLOS *Glossopteridales*, CAYT *Caytoniaceae*, ANGI angiosperms, PENT *Pentoxylon*, BENN *Bennettitales*, EPHE *Ephedra*, WELW *Welwitschia*, GNET *Gnetum*, CONIF coniferopsids, MzSF Mesozoic "seed ferns," GNETS *Gnetales*. Tree rooted by specifying Devonian "progymnosperms" (not shown) as outgroup

If the original angiosperm carpel contained several anatropous, bitegmic ovules, as is widely assumed, it has no obvious prototype in other anthophytes. *Bennettitales* had a terminal ovuliferous receptacle covered with numerous orthotropous ovules and interseminal scales, whereas female flowers of *Gnetales* have a single orthotropous ovule surrounded by a second integument that apparently corresponds to the perianth of the male flower (CRANE 1985). A possible carpel prototype occurs in *Caytonia*, which had ovulate structures consisting of a rachis bearing two rows of anatropous cupules, each containing several ovules. The cupules themselves would be derived from leaflets with ovules on their adaxial surface (HARRIS 1940, REYMANÓWNA 1974). If the number of ovules per cupule was reduced to one, each cupule would be comparable to an anatropous, bitegmic ovule; the carpel might correspond to the rachis, expanded and folded to enclose the cupules (GAUSSEN 1946, STEBBINS 1974, DOYLE 1978). In *Bennettitales*, CRANE (1985) and DOYLE & DONOGHUE (1986) proposed that *Caytonia*-like sporophylls were reduced to single orthotropous ovules (which are at least sometimes bitegmic, suggesting that they are also cupules) and sterilized to produce the interseminal scales. In *Gnetales*, the number of ovules per flower would be reduced to only one, and the cupule wall would be lost (a possible weakness of this scheme, discussed further below). Microsporophylls would be reduced in both angiosperms (to stamens with two lateral pairs of microsporangia, considered synangia) and *Gnetales*, where *Welwitschia* probably shows the basic condition, with a cup-like androecium representing either a whorl of six microsporophylls (CRANE 1985, 1988; DOYLE & DONOGHUE 1986, 1992) or more likely two opposite microsporophylls with three synangia each (NIXON & al. 1994). Assuming that the cupule-bearing structures of *Caytonia* are sporophylls, this scenario is a classical euanthial theory (where the flower is an axis bearing sporophylls), reminiscent of ARBER & PARKIN (1907, 1908) but with stronger character support and more specific details on the relatives of anthophytes and the homologies of floral parts.

Two related alternatives may be mentioned at this point. First, DOYLE & DONOGHUE (1986: 363) and CRANE (1988: 253) discussed the possibility that the ovuliferous receptacle of *Bennettitales* is not an axis but rather a megasporophyll, shifted to a terminal position and modified into a radial structure. Such a structure might be analogous to the developmentally terminal single carpel of *Tasmannia* (*Drimys*) *lanceolata* (*Winteraceae*) (TUCKER & GIFFORD 1966). Second, MEYEN (1988) suggested that angiosperms were derived from *Bennettitales* by gamoheterotopy (transfer of characters from one sex to another). Although multiovulate angiosperm carpels are very different from the structures on a bennettitalean ovuliferous receptacle, such carpels are more like bennettitalean microsporophylls, which were often flat and bore two rows of adaxial synangia. A regulatory mutation that led to remodeling of female structures on the microsporophyll plan, with bitegmic ovules in place of microsynangia, could provide a prototype for the angiosperm flower.

In a subsequent analysis of angiosperms, concentrating on "magnoliid" groups and representing more advanced taxa with reconstructed ancestors or relatively primitive placeholders, DONOGHUE & DOYLE (1989) used the outgroups found in the seed plant analysis to polarize characters within angiosperms. The resulting trees were "rooted" in or next to *Magnoliales* in a restricted sense (those families

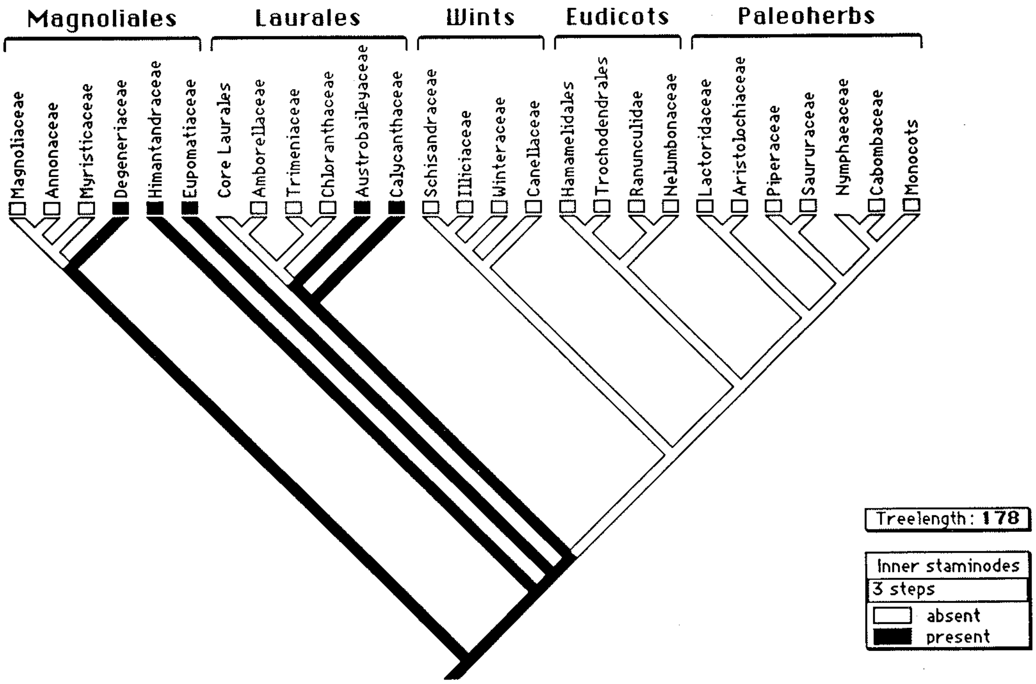


Fig. 2. Representative most parsimonious angiosperm tree of Donoghue & Doyle (1989), showing distribution of the inner staminode character. Core Laurales *Hortonia*, *Monimiaceae*, *Atherospermataceae*, *Siparunaceae*, *Gomortega*, *Hernandiaceae*, *Lauraceae*; Wints winteroids. In other most parsimonious trees, *Magnoliales* are a monophyletic group and include *Canellaceae*, but in this tree *Magnoliales* are paraphyletic and *Canellaceae* belong to the winteroid clade

with granular exine structure), which formed either a basal clade or a paraphyletic basal grade (e.g., Fig. 2). The remaining angiosperms included two other woody magnoliid lines (*Laurales* and winteroids, including *Winteraceae*, *Illiciales*, and possibly *Canellaceae*, which are basal *Magnoliales* in other most parsimonious trees), in uncertain order, then a clade consisting of groups with tricolpate and derived pollen, called eudicots by Doyle & Hotton (1991), linked with a clade consisting of herbaceous magnoliids (*Aristolochiaceae*, *Lactoridaceae*, *Nymphaeales*, and *Piperales*, not including *Chloranthaceae*, which belong to *Laurales*) and monocots, called paleoherbs. These results can be related to three models for the primitive flower discussed by Endress (1986): *Chloranthaceae*, with extremely simple flowers; *Winteraceae*, with variable numbers of irregularly arranged parts; and *Austrobaileyaceae*, *Himantandraceae*, and *Eupomatiaceae*, with inner staminodes. The Donoghue & Doyle trees are most consistent with the third model, since as shown in Fig. 2 the taxa with inner staminodes are at or near the base of *Magnoliales* and *Laurales*, and least consistent with the chloranthaceous model; trees with *Chloranthaceae* basal are seven steps longer. The third model is also favored by the analysis of Loconte & Stevenson (1991), which placed *Calycanthales* (*Calycanthaceae* plus *Idiospermaceae*), with inner staminodes, at the base of the angiosperms.

Doyle & Donoghue (1986) and Donoghue & Doyle (1989) recognized that these results were uncertain, since in both studies they had found very different trees that were almost equally parsimonious. They also knew that the results could be incorrect due to circular reasoning. In the seed plant analysis, angiosperms were scored based on the assumption that they were originally like *Magnoliales* or *Winteraceae*. However, if this assumption was incorrect, it may have led to incorrect placement of angiosperms in the seed plant trees, and this would have led to an inappropriate choice of outgroups in the angiosperm analysis. Thus it is possible that the basal position of *Magnoliales* in the angiosperm trees was a consequence of the earlier assumption that the first angiosperms were like this group. If different outgroups had been used, another group might have been basal in angiosperms, and the inferred primitive flower might have been different.

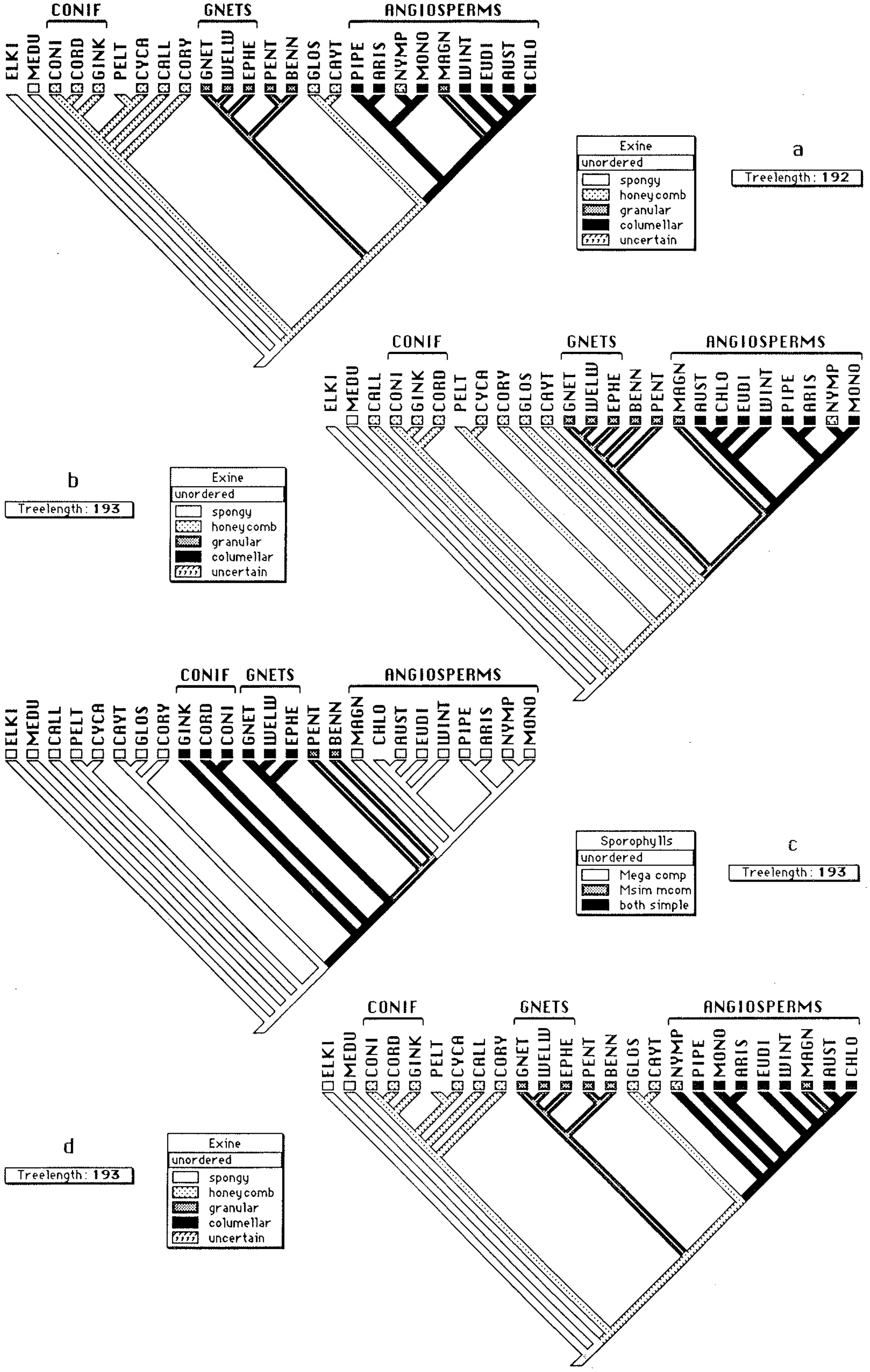
These doubts were increased by analyses of rRNA sequence data (HAMBY & ZIMMER 1992, DOYLE & al. 1994), which indicate that the angiosperms are not rooted among *Magnoliales* and other woody magnoliids, but rather among paleoherbs, with *Nymphaeales* basal. Suggestively, a similar rooting was only one step less parsimonious than the magnolialean rooting in terms of the morphological data set of DONOGHUE & DOYLE (1989). In trees based on *rbc*L (cpDNA) sequences (CHASE & al. 1993, QIU & al. 1993), the angiosperms are rooted between the aquatic genus *Ceratophyllum* and all the other groups, which then split into eudicots and a monosulcate clade (monocots and magnoliids).

Fossil data also raise doubts concerning the magnolialean rooting, since monocots, other probable paleoherbs, and uniovulate carpels resembling those of *Chloranthaceae* are conspicuous in the early record of angiosperms (HICKEY & DOYLE 1977, TAYLOR & HICKEY 1990, CRANE & al. 1994, FRIIS & al. 1994). However, these observations do not clearly favor any alternative rooting, since the oldest angiosperm-containing floras (Barremian-Aptian) also provide evidence of clades whose modern representatives are woody and usually have multiovulate carpels (*Magnoliales*, winteroids: DOYLE & HOTTON 1991, DOYLE & DONOGHUE 1993), and the abundance of uniovulate carpels could be largely a function of the early radiation of *Chloranthaceae* and related *Laurales*.

To address these problems, DOYLE & DONOGHUE (1990) and DOYLE & al. (1994) conducted a new seed plant analysis with a greater sample of angiosperm diversity, specifically nine potentially basal angiosperm groups, included both individually and together. When *Magnoliales* were substituted for angiosperms as a whole, results of the previous sort were obtained, as might be expected, but substituting other groups for angiosperms or including all nine angiosperm taxa changed the inferred relationships among angiosperms and other seed plants. However, in the nine-angiosperm analyses, trees like those found by DOYLE & DONOGHUE (1986) and several others were only one step less parsimonious than the shortest trees. While these results do not strongly refute the previously proposed euanthial scenario, they do imply that there are several other very different pathways of floral evolution that must also be considered.

Challenges to the anthophyte concept

Trees found by DOYLE & al. (1994) and recent observations on Mesozoic seed plants raise the possibility that flower-like structures evolved independently in angiosperms and other anthophyte groups. Some of the fossil data may be consistent with a single origin of the flower, but they raise questions concerning the homologies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of ovule-bearing structures postulated by Crane (1985) and Doyle & Donoghue (1986) (Fig. 1).

Flowers would clearly arise more than once in alternative trees in which anthophytes and derived polyphyletically from Mesozoic seed ferns. Trees of this sort, with angiosperms linked directly with *Caytonia* and the resulting clade linked with *Bennettitales*, *Pentoxylon*, and *Gnetales*, were one step less parsimonious than the shortest trees in terms of the data sets of Doyle & Donoghue (1986, 1992). However, this situation was reversed in the nine-angiosperm analysis of Doyle & al. (1994): in the most parsimonious trees, angiosperms were linked with *Caytonia* and glossopterids (Fig. 3a), and trees of the previous kind were one step longer (Fig. 3b). Similar trees (with various relationships of *Caytonia* and glossopterids) were found in several of the analyses in which individual groups were substituted for angiosperms (*Nymphaeales*, monocots, *Aristolochiaceae*, tricolpate eudicots, *Winteraceae*, *Austrobaileya*). These results take on special relevance in light of rRNA analyses, which place one of these groups, *Nymphaeales*, at the base of the angiosperms (Hamby & Zimmer 1992, Doyle & al. 1994).

The change in relative status of these trees reflects the ambiguity of character support for the anthophyte clade. Although Doyle & Donoghue (1986: 353) showed 10 characters uniting the anthophytes, four of these could have arisen lower on the tree, because their state is unknown in fossil outgroups (tunica layer in the apical meristem, scalariform pitting in the secondary xylem, lignin showing Mäule reaction, siphonogamy). Two are equivocal as synapomorphies because of variation in the outgroups or within anthophytes: simply pinnate leaves could have arisen below glossopterids, with a reversal to pinnately compound leaves in *Caytonia*; syndetocheilic (paracytic) stomata could have arisen at the base of anthophytes and been lost in *Pentoxylon* and *Ephedra*, or evolved independently in angiosperms, *Bennettitales*, and the *Welwitschia-Gnetum* clade. The four unequivocal synapomorphies were once-pinnate microsporophylls, one ovule per cupule (bitegmic ovule), loss of air sacs on the pollen, and granular or columellar exine structure, but the first three of these depend on outgroup relationships (e.g., whether anthophytes are nested among groups with saccate pollen, like *Caytonia* and glossopterids). Furthermore, there are competing characters that potentially unite angiosperms with *Caytonia* (flat guard cells) or *Caytonia* and glossopterids (reticulate venation, anatropous cupules).

Fig. 3. Most parsimonious and one step less parsimonious seed plant trees found in the nine-angiosperm analyses of Doyle & al. (1994). PIPE *Piperales* (*Piperaceae*, *Saururaceae*); ARIS *Aristolochiaceae*; NYMP *Nymphaeales* (*Nymphaeaceae*, *Cabombaceae*); MONO monocots; MAGN "core" *Magnoliales* (*Magnoliaceae*, *Degeneriaceae*, *Myristicaceae*, *Annonaceae*); WINT *Winteraceae*; EUDI eudicots (groups with tricolpate and derived pollen); AUST *Austrobaileyaceae*; CHLO *Chloranthaceae*; other abbreviations as in Fig. 1. *a* Representative most parsimonious tree, with angiosperms linked directly with *Caytonia* and glossopterids; *b* tree with previously most parsimonious arrangement of non-angiosperm groups, as in Fig. 1, with anthophytes linked with *Caytonia* and *Magnoliales* basal in angiosperms; *c* neo-englerian tree, with anthophytes linked with coniferopsids and *Gnetales* basal in anthophytes; *d* angiosperms rooted among paleoherbs, with basal groups arranged as implied by rRNA data (Doyle & al. 1994)

Factors favoring the shift to the tree in Fig. 3a include elimination of the distinction between once-pinnate and pinnately compound microsporophylls (Doyle & Donoghue 1992) and changes in two pollen characters that were needed in order to remove biases in the previous analyses. Granular and columellar infratectal structures were combined as one state in the seed plant analysis (Doyle & Donoghue 1986) but split in the angiosperm analysis (Donoghue & Doyle 1989), with granular designated as ancestral. This implicitly treated honeycomb alveolar, granular, and columellar as an ordered series, which would bias against direct derivation of columellar from alveolar structure, as in trees where angiosperms are linked with alveolar outgroups like *Caytonia* and glossopterids, and columellar taxa like most paleoherbs are basal in angiosperms. Similarly, Donoghue & Doyle (1989) recognized two endexine states in the angiosperm analysis, with absence of extra-apertural endexine (as in *Magnoliales*) designated as ancestral, and hence closer to the laminated endexine condition of gymnosperms. Since these biases are hard to justify, Doyle & al. (1994) redefined these characters as unordered, contributing to the new result. Another factor was the inclusion of angiosperm taxa with anomocytic as well as paracytic stomata (paleoherbs, eudicots). Doyle & al. (1994) added one new character shared by angiosperms and *Gnetales*, double fertilization (fusion of both sperm with megagametophyte nuclei, with or without endosperm formation, as documented in *Ephedra* by Friedman 1990, 1992), but this is equivocal as an anthophyte synapomorphy because its state is unknown in fossils.

Since *Bennettitales*, *Pentoxylon*, and *Gnetales* are still the next-closest relatives of angiosperms, trees like Fig. 3a could be thought of as implying that *Caytonia* and/or glossopterids are anthophytes, rather than as breaking up the anthophytes. However, because there is no evidence that the relatively large, complex sporophylls of *Caytonia* and glossopterids were aggregated into typical flowers, the flower would have evolved independently in angiosperms and the bennettitalean-gnetalean line. An important point is that these trees implicitly assume that *Caytonia* and glossopterids had anthophyte states in characters that are unknown in fossils (tunica, Mäule reaction, siphonogamy, double fertilization). The lack of independent evidence for this assumption could be regarded as a weakness of this scheme, although it is not wholly implausible in view of the small size and anthophyte-like anatomical features of *Caytonia* seeds (reduced megaspore wall, thick nucellar cuticle: Harris 1954, Reymanówna 1974, 1974; Crane 1985).

Even if anthophytes as a group are monophyletic, there are growing indications that flowers may have arisen more than once among them, or at least evolved from a rather different prototype than the one postulated by Doyle & Donoghue (1986). In other words, anthophytes may be a valid clade, but their name may be inappropriate.

In *Bennettitales*, Crane (1988) showed that reports of bisexual flowers in the oldest (Late Triassic) representatives are questionable, and his preliminary phylogenetic analysis indicated that bisexual flowers were derived within the order. Several forms apparently lacked a perianth. Furthermore, the Triassic fossil *Westersheimia* consists of several ovuliferous receptacles rather than a single terminal one, with no sign of other floral parts. It is not clear whether this structure was a branch bearing several flowers or a pinnately compound appendage, but the latter interpretation would support the concept that the ovuliferous receptacle of other *Bennettitales* was a secondarily terminal, radial megasporophyll, rather than an axis with reduced, uniovulate (unicupulate) megasporophylls. Triassic microsporophylls called *Leguminanthus* had broad, sheathing bases, implying that they are not basally fused like the microsporophylls of most *Bennettitales*, and probably not whorled. If this condition was basic in *Bennettitales*, it would negate one of the apparent synapomorphies (whorled microsporophylls) that link *Bennettitales* and *Gnetales* in the analyses of DOYLE & DONOGHUE (1986, 1992).

The reproductive structures of *Pentoxylon* have never seemed very flower-like, although this could be a result of loss of parts: they consist of branched microsporophylls and pedunculate "heads" of ovules (*Carnoconites*) that were borne on separate short shoots, with no associated perianth. CRANE (1985) and DOYLE & DONOGHUE (1986) interpreted *Carnoconites* as an axis with reduced uniovulate megasporophylls, like the ovuliferous receptacle of *Bennettitales.* However, although this interpretation is consistent with the morphology of *C. cranwelliae*, which had single heads on unbranched peduncles, CRANE (1988: 253) pointed out that it is questionable for *C. compactus*, which had branched peduncles with several heads. This suggests rather a compound sporophyll with ovule-bearing pinnae, possibly comparable to *Westersheimia.* Finally, ROTHWELL & SERBET (1994) have found that heads of *Carnoconites* have bilateral internal anatomy, also implying that they are foliar structures rather than axes bearing reduced sporophylls.

In *Gnetales*, the most significant new data come from observations by KIRCHNER (1992) and VAN KONIJNENBURG-VAN CITTERT (1992) on *Piroconites kuespertii*, an Early Jurassic fossil in which VAN KONIJNENBURG-VAN CITTERT found typically gnetalean striate ephedroid pollen, and associated organs, here referred to collectively as *Piroconites. P. kuespertii* is a scale-like structure with numerous trilocular synangia on its upper surface, which is sometimes found attached to the adaxial surface of a lanceolate, parallel-veined bract (*Chlamydolepis lautneri*). These bracts are somewhat similar to the putatively associated leaves (*Desmiophyllum gothanii*). The individual synangia are reminiscent of the trilocular microsynangia of *Welwitschia*, but *Welwitschia* has only three synangia per microsporophyll (assuming that the androecium consists of two opposite sporophylls: NIXON & al. 1994). The female structures (*Bernettia inopinata*) appear to be constructed on a similar plan, but the ovule-bearing portion has numerous ovules in the place of microsynangia and is always associated with the bract (KIRCHNER 1992, VAN KONIJNENBURG-VAN CITTERT, pers. comm.; and my own observations on material at Utrecht). How these organs were borne is unknown, but *Piroconites* specimens are often preserved next to each other, suggesting that they were associated on the plant (van KONIJNENBURG-van CITTERT 1992). They may thus have formed flower-like structures, but these would have been much larger and probably less tightly integrated than flowers of modern *Gnetales.*

The Late Triassic genus *Dechellyia* (ASH 1972) also seems related to *Gnetales*, based on its ephedroid pollen and opposite, linear leaves with two or four parallel veins, but it differs from the modern genera in having superficially conifer-like male strobili and conspicuously winged seeds borne oppositely at the tips of branches. These structures are not obviously comparable to those of *Piroconites*, although the winged seeds might be derived from a *Bernettia*-like prototype by

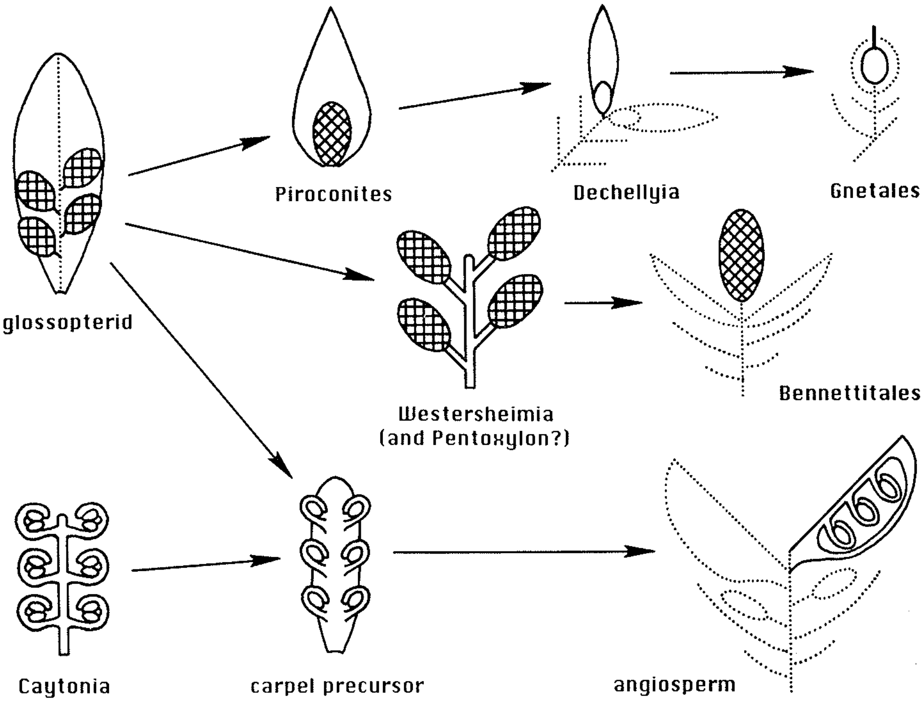

Fig. 4. Alternative scenarios for evolution of anthophyte ovulate structures suggested by the Jurassic gnetalean relative *Piroconites* (*Bernettia*) (Kirchner 1992, van Konijnenburg-van Cittert, 1992), the Triassic gnetalean relative *Dechellyia* (Ash 1972), and the compound ovuliferous receptacles of the Triassic bennettitalean *Westersheimia* (Crane 1988)

reduction of the number of ovules to one and modification of the subtending bract into the wing.

Considering potential outgroups of the anthophytes, the ovule-bearing structures of *Piroconites* (*Bernettia*) are unexpectedly similar to those of Permian glossopterids, suggesting the comparisons presented in Fig. 4. Glossopterid fructifications consist of one or more "cupules" with densely packed ovules on their adaxial surface (confirmed by orientation of the vascular bundles: Taylor & Taylor 1992), which are themselves attached to the midrib of a subtending leaf. As recognized by Retallack & Dilcher (1981), the morphological relationship of the cupule to the subtending leaf is problematical: it could be an appendage on a reduced branch in the axil of the leaf (cf. Meeuse 1976), a sporophyll adnate to the leaf (analogous to fusion between stamens and petals in angiosperms), or part of the leaf itself (analogous to the adaxial fertile segment of the leaf in the fern order *Ophioglossales*, and possibly also represented in the Cretaceous "seed fern" *Ktalenia* of Taylor & Archangelsky 1985, cf. Doyle & Donoghue 1986: 362). Any of these interpretations might also apply to the bract-sporophyll complex of *Piroconites*; better evidence on the morphological relationship of parts in the two groups could strengthen or refute their potential homology. Whatever its homologies, a whole

Bernettia-like structure would have to be reduced to a single terminal ovule between *Piroconites* and modern *Gnetales*. *Dechellyia* might represent an intermediate stage in this process, with the subtending bract still present as the wing. The morphological gap between these forms and modern *Gnetales* parallels the stratigraphic gap between Triassic-Early Jurassic ephedroid pollen (apparently representing stem-relatives of the group) and its better-documented Early Cretaceous radiation (which apparently involved crown-group *Gnetales*: DOYLE & DONOGHUE 1993).

This concept might also be extended to *Bennettitales* and *Pentoxylon*, although less easily. A glossopterid cupule or *Bernettia*, with densely packed ovules, might be compared with an ovuliferous receptacle of *Bennettitales* or a head of *Pentoxylon*, under the hypothesis discussed above that these structures are sporophylls shifted to a terminal position rather than axes bearing numerous reduced sporophylls. This might involve "spread" of the ovules to both sides of the cupule and thickening of the intervening tissue. As noted by VAN KONIJNENBURG-VAN CITTERT (1992), *Piroconites* is also reminiscent of *Bennettistemon ovatum*, a bennettitalean microspororophyll with numerous densely packed microsporangia. However, unlike *Piroconites*, *Bennettitales* and *Pentoxylon* have no obvious homolog of the subtending leaf of glossopterids, which would have to be lost or otherwise dissociated from the ovuliferous structure. A still greater obstacle is the presence of a "cupule" around the ovule of some *Bennettitales* and possibly *Pentoxylon* (HARRIS 1954, CRANE 1985, 1988). In the schemes of CRANE (1985) and DOYLE & DONOGHUE (1986, 1992; Fig. 1), this layer is homologous with the cupule of *Caytonia*, glossopterids, and corystosperms. Under this interpretation, the ovuliferous receptacle could correspond to a glossopterid structure bearing several cupules, but not to a single glossopterid cupule or ovule-bearing structure of *Piroconites*.

How angiosperms might relate to this scheme is unclear (Fig. 4). A key requirement is to explain both the carpel and the presence of two ovule integuments (this is a weakness of the anthocorm theory of MEEUSE 1976, which homologizes the cupule of Mesozoic seed ferns with the carpel, leaving no homolog for the second integument). One possibility is that anthophytes are monophyletic but more closely related to glossopterids than to *Caytonia*. The angiosperm carpel might then be derived by conversion of glossopterid cupules into bitegmic ovules (by reduction to one ovule per cupule) and enclosure by folding of the subtending leaf (STEBBINS 1974, RETALLACK & DILCHER 1981). Another possibility is that anthophytes are diphyletic, with *Bennettitales*, *Pentoxylon*, and *Gnetales* related to glossopterids and angiosperms related to *Caytonia*. The carpel could then be derived from a *Caytonia*-like prototype by expansion of the rachis and reduction of the cupules to bitegmic ovules (GAUSSEN 1946, DOYLE 1978, CRANE 1985, DOYLE & DONOGHUE 1986). However, unless glossopterids and *Caytonia* had more aggregation of fertile parts than seems likely, both schemes would imply that flower-like structures evolved independently in angiosperms and other anthophytes.

None of these schemes would rule out some sort of relationship between glossopterids and *Caytonia*, since these groups are more or less closely related in previous analyses, based on simple-reticulate leaf venation, seed characters (small size, platyspermy, thick nucellar cuticle), and saccate pollen, and their cupules might be ultimately homologous. The main problem is the fact that the ovulate structures of glossopterids are attached to a subtending leaf, but there is no evidence for such an association in *Caytonia* (Doyle & Donoghue 1986: 362–363). One possibility is that the glossopterid condition was ancestral, and the leaf was lost or reduced to form the sporophyll rachis in the *Caytonia* line. Another is that the ancestral structure was a cupule-bearing structure more like that of *Caytonia*, which became associated with the leaf in the glossopterid line. Better evidence on the morphological nature of structures in glossopterids and *Caytonia* and/or discovery of more primitive relatives of these groups would be most welcome.

Neo-englerian scenarios

A very different alternative is that anthophytes are related not to Mesozoic seed ferns but rather to coniferopsids. Trees of this sort, called neo-englerian because they recall the early twentieth century German-Austrian view that angiosperms are derived from conifers via *Gnetales* (e.g., Wettstein 1907), were only two steps less parsimonious than the shortest trees in terms of the data set of Doyle & Donoghue (1986), and basically similar trees have been found by Nixon & al. (1994) and Rothwell & Serbet (1994). Coniferopsids have reduced, simple leaves and sporophylls relative to the first seed plants (seed ferns). In most (though not all) neo-englerian trees, the basal group in anthophytes is not angiosperms but *Gnetales*, which resemble coniferopsids in having linear leaves (except *Gnetum*, which is apparently derived) and reduced sporophylls, and Mesozoic seed ferns form a clade located elsewhere on the tree. In terms of the nine-angiosperm data set of Doyle & al. (1994), some neo-englerian trees were only one step less parsimonious than the shortest trees (Fig. 3c). Neo-englerian trees were also found when *Chloranthaceae* were substituted for angiosperms, as might be expected based on the presence of several "gnetalean" features in this family, such as opposite leaves, two-trace nodes, spicate inflorescences of simple flowers, and carpels with one orthotropous ovule (cf. Doyle & Donoghue 1986: 386). In the trees of Nixon & al. (1994), angiosperms are actually nested within *Gnetales* and therefore derived from a gnetalean ground plan.

Neo-englerian trees seem more plausible if groups with simple flowers and orthotropous ovules (such as *Chloranthaceae*, *Piperales*, or *Ceratophyllum*) are assumed to be basal in angiosperms, which is the case in the trees of Taylor & Hickey (1992), Chase & al. (1993), and Nixon & al. (1994). However, this was not the sort of arrangement seen in neo-englerian trees derived from the nine-angiosperm data set of Doyle & al. (1994): instead, the basal angiosperm group was *Magnoliales* (Fig. 3c). This counterintuitive result seems to follow from the fact that *Magnoliales* are actually more like *Gnetales* than *Chloranthaceae* are in many characters, such as absence of chloranthoid marginal teeth on the leaves and boat-shaped pollen with a continuous tectum and granular exine structure. Nine-angiosperm trees with *Chloranthaceae* basal are much less parsimonious, by five steps.

Neo-englerian trees have very different implications for homologies of angiosperm reproductive structures (Fig. 5). The original organization would presumably be that seen in cordaites and Paleozoic conifers: a compound strobilus consisting of an axis with bracts and axillary fertile short shoots bearing scale leaves and simple sporophylls, with either a few microsporangia or an ovule with one integument. Subsequently, the ovuliferous axillary shoots were transformed into the cone scales

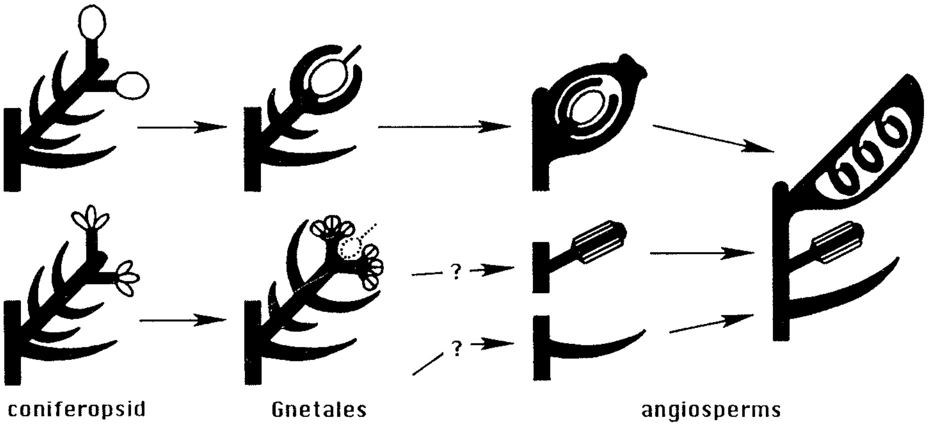

Fig. 5. Scenario for evolution of angiosperm reproductive structures implied by neo-englerian trees (Fig. 3c), with anthophytes linked with coniferopsids and angiosperms derived from a gnetalean prototype by aggregation of bracts and axillary fertile shoots. Position of the abortive ovule in the male flower of *Welwitschia* indicated by dotted lines

of modern conifers (FLORIN 1951). Within anthophytes, the basic condition would be one ovule per short shoot, as in *Gnetales*. Within *Gnetales*, Fig. 5 assumes that the basic morphology was most like that of *Welwitschia*, as argued by CRANE (1985, 1988), based on the detailed observations of MARTENS (1971): male flower with two pairs of perianth parts and two microsporophylls; female flower with an ovule with a micropylar tube, surrounded by an outer integument corresponding in position to the inner perianth pair in male flower, plus an outer perianth pair. The male flower of *Welwitschia* has an abortive terminal ovule, but because this could be either a vestige from a bisexual ancestor (ARBER & PARKIN 1908) or an autapomorphy, it is indicated with dotted lines (this ovule is unitegmic, which is an argument for homology of the outer integument in the female flower with the perianth). In general, conditions in other *Gnetales* can be ascribed to reduction. *Ephedra* has one pair of perianth parts in the male flower and no appendages other than the outer integument in the female flower (this develops from two lateral primordia and may therefore correspond to the outer rather than the inner perianth pair of *Welwitschia*: TAKASO 1985). *Gnetum* has a simple perianth in the male flower but two outer integuments in the female flower, perhaps corresponding to both perianth pairs in *Welwitschia*.

Not all of these homologies are clearcut, so other interpretations should be kept in mind. One problem is the presence of two small nubs on either side of the terminal ovule in the male flower of *Welwitschia* (MARTENS 1971). In the context of their trees, DOYLE & DONOGHUE (1986: 416) surmised that these nubs might be vestiges of the *Caytonia*-anthophyte cupule or of bennettitalean interseminal scales (another possible homology, suggested by the comparisons made in the previous section, is with the leaf or wing associated with the ovulate structures of *Piroconites* and *Dechellyia*: Fig. 4). In contrast, FRIIS (pers. comm.) suggests that they are reduced bracts (perianth parts, in the present terminology), like those making up the outer integument in the female flower. However, this would imply that the male flower is an axis bearing both microsporophylls and a structure corresponding to a whole female flower, or else a single axis bearing sterile appendages, microsporophylls, sterile appendages, and a terminal ovule, a sequence with no known parallels in coniferopsids. Furthermore, since the two nubs are lateral, they would correspond in position to the outer perianth pair of the female flower, implying that the inner perianth pair was lost. A weakness of the CRANE (1985) and DOYLE & DONOGHUE (1986) schemes is the fact that they must assume that the original cupule of *Caytonia* and *Bennettitales* was lost in *Gnetales*; however, the FRIIS scenario must assume equally major losses.

Assuming the gnetalean prototype postulated in Fig. 5, I would envision two very different scenarios for evolution of a typical bisexual angiosperm flower.

One scenario would involve transformation of a coniferopsid-gnetalean axillary fertile short shoot into an angiosperm flower by elaboration of its component parts. Like the schemes discussed in the first section, this is basically a euanthial interpretation. Floral parts are borne in the same order in a bisexual angiosperm flower and the male flower of *Welwitschia*, but they are much simpler in the latter. It is not too difficult to imagine transformation of scale-like microsporophylls with a few free microsporangia into stamens with two lateral synangia; the microsporophylls of *Welwitschia*, with three synangia, might represent an intermediate step. However, carpels enclosing several bitegmic ovules would have to be derived from single unitegmic ovules, which are borne on stalk-like sporophylls in some cordaites but completely sessile in modern conifers and *Gnetales*. Both the carpel and the outer integument of the ovules would presumably have to arise de novo. The need to assume so much de novo origin of structures is in itself reason to question this scenario.

The other scenario would involve aggregation of several bracts and short shoots into a superficially flower-like but actually multiaxial structure. This is a pseudanthial interpretation, as proposed by WETTSTEIN (1907) and reformulated by MEEUSE (1972, 1976) in terms of "advanced cycadopsid" groups (especially Mesozoic seed ferns and *Gnetales*, interpreted as having axes with bracts and axillary fertile structures – a reasonable interpretation for *Gnetales* but questionable for *Caytonia*, in which the fertile structures appear to be pinnately organized sporophylls: HARRIS 1940, REYMANÓWNA 1974, DOYLE 1978, CRANE 1985). However, an updated version would not rely on WETTSTEIN's assumption that "*Amentiferae*" are primitive angiosperms, since these are now generally recognized to be advanced eudicots. A pseudanthial scenario seems easiest to envision if the original angiosperm carpel had one orthotropous ovule, as in *Chloranthaceae*, *Piperaceae* (although here the unilocular ovary appears to consist of three or four fused carpels: TUCKER & al. 1993), or *Ceratophyllum*. The outer integument might be homologous with the outer integument of *Gnetales*, and hence with the perianth of the male flower and the scale leaves on the axillary short shoot of cordaites and Paleozoic conifers. The carpel wall might be the subtending bract, expanded and folded around the axillary unit. As recognized by TAYLOR (1991) in postulating a similar carpel prototype, subsequent elaboration would be required to produce other kinds of carpel: ovules would have to be multiplied along the ventral margins of the carpel (bract) and reflexed into an anatropous orientation.

The position and morphology of the stamens in a bisexual angiosperm flower pose additional problems for a pseudanthial interpretation. This is because microsporophylls do not occupy the appropriate position in *Gnetales* if the flower is homologized with a whole compound strobilus. In the male flower of *Welwitschia*, the microsporophylls are located between the abortive unitegmic ovule and the perianth, which corresponds to the outer integument in the female flower. The same arrangement occurs in occasional bisexual flowers of *Ephedra* (MEHRA 1950, CRANE 1985). Under the scheme in Fig. 5, the corresponding position for the stamens in an angiosperm would be between the inner and outer integuments of the ovule, not below the carpels on the floral axis (the primary axis of the compound strobilus). One interpretation that would place stamens and carpels on the same axis is that each stamen represents a whole gnetalean male flower (cf. WETTSTEIN 1907). However, this would require transformation of a stem-like radial structure with a perianth and sporophylls into a single bilateral stamen with a microsynangium on either side. The subtending bract would also have to be accounted for, whether by loss, fusion with the axillary shoot to become part of the stamen, or transformation into a perianth part. The last hypothesis might be plausible for angiosperms that have stamens opposite the petals, but it would require dissociation of the two structures in other groups. Another interpretation is that the angiosperm stamen corresponds to a single gnetalean microsporophyll that was shifted from one order of branching to another (from the axillary short shoot to the primary axis of the compound strobilus) – an example of heterotopy.

Given the association of angiosperms, *Gnetales*, and *Bennettitales* in all recent analyses, any interpretation of the angiosperm flower must also be consistent with origin of the bennettitalean flower. The similar order of parts in male flowers of *Welwitschia* and bisexual flowers of *Bennettitales* would be consistent with an elaboration scenario, but this would require transformation of simple microsporophylls into complex structures with pinnately arranged synangia (i.e., even more elaboration than in angiosperms), de novo origin of the cupule, and multiplication of the ovules, plus origin of the interseminal scales. A pseudanthial scenario would pose a different set of problems, particularly in explaining why the organization of the so-called flowers of *Gnetales* and *Bennettitales* should seem so similar if the bennettitalean flower is actually an aggregation of gnetalean bracts and short shoots. FRIIS (pers. comm.) suggests that the cupule of *Bennettitales* is homologous with the outer integument (perianth) of *Gnetales*, which would imply that the ovuliferous receptacle is an axis bearing fertile shoots (although without clearly identifiable subtending bracts, unless these are represented by the interseminal scales). This would fit her view that the ovule in the male flower of *Welwitschia* is reduced, but it implies a serial juxtaposition of leaf-like pinnate microsporophylls and secondary ovuliferous shoots on the same axis. This poses essentially the same problems discussed in attempting to explain the bisexual flower of angiosperms as a pseudanthium, although if angiosperms and *Bennettitales* are related, the necessary reorganization might have occurred only once, in their common ancestor.

A general reason to be suspicious of neo-englerian scenarios is that there may be an intrinsic bias in favor of them at the stage of character analysis (DOYLE & DONOGHUE 1986: 373). Whereas trees linking anthophytes with Mesozoic seed ferns assume that the more complex, pinnately organized leaves and sporophylls of angiosperms, *Bennettitales*, and Mesozoic seed ferns are homologous and the simpler leaves and sporophylls of coniferopsids and *Gnetales* are convergent, neo-englerian trees assume that the simple organs are homologous and the complex organs are convergent. However, simple structures look intrinsically more similar than complex structures, even if they are derived (reduced) from very different precursors. In other words, it is easier to go wrong in homologizing reduced structures than complex ones, and therefore to err in favor of trees of the neo-englerian type. Nevertheless, whether the convergences are between coniferopsids and *Gnetales* or between other anthophytes and Mesozoic seed ferns, the repeated appearance of trees linking anthophytes with Mesozoic seed ferns and with coniferopsids implies that both sorts of tree should be taken seriously.

Paleobotanical and molecular tests

In searching for data that might provide a test of these alternatives, it should be noted that all of the trees considered imply that the closest living relatives of angiosperms are *Gnetales*. This conclusion is confirmed by analyses of rRNA and *rbc*L (cpDNA) sequences (Hamby & Zimmer 1992, Chase & al. 1993, Doyle & al. 1994) and strengthened by the embryological studies of Friedman (1990, 1992, 1994), which show that *Ephedra* resembles angiosperms in having not only double fertilization but also similar embryogeny: after two divisions of each diploid fusion nucleus (probably an autapomorphy), embryo development follows a typically angiosperm-like cellular pattern. Most of the radical differences in scenarios for floral evolution are a function of how fossil taxa (*Caytonia*, glossopterids, *Piroconites*, *Dechellyia*, *Bennettitales*, *Pentoxylon*) fit in around living angiosperms, *Gnetales*, and coniferopsids. On the one hand, this reaffirms the importance of fossils; on the other, it suggests what sorts of paleobotanical data we should look for.

Critical data on these problems could come from more complete material of known fossil taxa or from discovery of anthophytes with previously unknown character combinations. For example, determination that *Caytonia* had anthophyte states in characters that are now unknown would strengthen its relationship with the anthophytes and argue against neo-englerian trees, although it would not say whether anthophytes are monophyletic or diphyletic. Discovery that *Caytonia* did not have anthophyte states in these characters would strengthen the hypothesis that anthophytes are monophyletic, but whether they are related to Mesozoic seed ferns or to coniferopsids would remain unresolved. Among fossils that are less well known, *Piroconites* may pose problems for the euanthial interpretation shown in Fig. 1, but it seems even less consistent with neo-englerian trees, since its reproductive structures are much less coniferopsid-like than those of modern *Gnetales*. On the other hand, documentation of additional coniferopsid-like features in *Dechellyia* could have an opposite effect. It would be useful to know if *Piroconites* and *Dechellyia* had a tubular micropyle, one of the synapomorphies linking *Gnetales* and *Bennettitales* in the analyses of Doyle & Donoghue (1986, 1992). Further evidence on the plant that produced *Eucommiidites* pollen, another probable anthophyte (Pedersen & al. 1989), would also be of interest.

Discovery of any fossil that could be confidently placed on the stem-lineage leading to angiosperms could also resolve many questions. Thus the Late Triassic

Crinopolles pollen group (CORNET 1989), which has monocot-like graded reticulate sculpture, or the Middle Jurassic leaf *Phyllites* (SEWARD 1904), which has paleoherb-like palmate venation, could constitute evidence that the angiosperms are rooted near paleoherbs rather than *Magnoliales*, providing that these fossils are on the angiosperm stem-lineage, as proposed for *Crinopolles* based on their gymnosperm-like endexine (DOYLE & HOTTON 1991, DOYLE & DONOGHUE 1993). However, more evidence concerning other organs is needed before it can be assumed that these fossils are really related to angiosperms.

Although there has been great progress in understanding the diversity of Early Cretaceous angiosperm reproductive structures (cf. CRANE & al. 1994, FRIIS & al. 1994), it seems less likely that Cretaceous fossils will provide decisive evidence on these questions. This is because so far all Cretaceous angiosperm relatives appear to belong to the angiosperm crown-group, rather than being on the angiosperm stem-lineage (DOYLE & DONOGHUE 1993). They may therefore have a great deal to say about relationships within angiosperms, but less about outgroup relationships or ancestral states. However, this could change if it is found that taxa on the angiosperm stem-lineage persisted into the Cretaceous, or if sampling becomes exhaustive enough to establish that the very earliest Cretaceous angiosperms all had one type of floral morphology.

Even though the most obvious tests are paleobotanical, certain data from extant plants could help. For example, demonstration that the androecium of *Welwitschia* (and the androecial column of *Ephedra* and *Gnetum*) consists of two basically pinnate microsporophylls with three synangia each (NIXON & al. 1994), rather than a whorl of six simple microsporophylls, would remove one character (simple microsporophylls) supporting neo-englerian trees in the data sets of DOYLE & DONOGHUE (1986, 1992). However, the most promising new kinds of neontological data are molecular.

First, although molecular data may not show how fossils fit into seed plant phylogeny (barring recovery of DNA sequences from fossils), they may say something about rooting of the angiosperms and morphology of the primitive flower. For example, in the most recent analyses of rRNA sequences (DOYLE & al. 1994), angiosperms are rooted among paleoherbs, with *Nymphaeales* basal, then *Piperales* (not including *Chloranthaceae*), *Aristolochiaceae* plus monocots, and a clade consisting of woody magnoliids and eudicots, within which relationships are poorly resolved. This does not represent a severe conflict with morphological data: with the nine-angiosperm morphological data set of DOYLE & al. (1994), trees with this arrangement of basal groups are only one step less parsimonious than the shortest trees (Fig. 3d). DOYLE & al. (1994) did experiments to evaluate the relative strength of these results, using a simplified rRNA data set with 11 angiosperm taxa and bootstrap analysis (FELSENSTEIN 1985), which asks how often a given clade is seen in analyses based on characters sampled randomly from the original matrix. The strongest results are that both angiosperms and *Gnetales* are monophyletic, at extremely high bootstrap levels of 100% and 99%, and the two groups are related, at the 88% level. This contradicts trees of NIXON & al. (1994), in which angiosperms are nested within *Gnetales* (which are therefore paraphyletic). Within angiosperms, *Nymphaeales* are basal in only 54% of the bootstrap replicates, but some combination of paleoherbs is almost always basal. *Magnoliales* are almost never basal, except at chance levels (less than 1%), and the same is true of *Chloranthaceae*.

These results call into question the use of *Magnolia* as a model for the primitive flower, but they do not support a radically different prototype (Doyle & al. 1994). *Piperales*, which have orthotropous ovules and no perianth and figure prominently in recent pseudanthial theories (Meeuse 1972, 1976), are low on the tree, but not basal. *Chloranthaceae* are still higher in the tree, supporting the view that their simple flowers are reduced. Instead, the arrangement of taxa implies that the primitive flower was more like that of *Cabomba*, *Lactoris*, *Saruma*, and monocots: trimerous and bisexual, with a perianth, stamens differentiated into anther and filament, and carpels with several anatropous ovules. However, position of the ovules might have been laminar rather than marginal (the most common condition in angiosperms), since Taylor (1991) characterizes placentation in *Nymphaeales* as lateral (along the radial walls of the carpel), chaotic, or even exmedial (on the carpel midrib). The seeds might have contained both perisperm and endosperm, an unusual feature of both *Nymphaeales* and *Piperales*. Looking outside the angiosperms, the inference that carpels originally had several anatropous ovules would conflict with neo-englerian pseudanthial schemes of the sort shown in Fig. 5, where the original carpel had a single orthotropous ovule. On the other hand, the possibility that placentation was originally laminar or exmedial rather than marginal might make it easier to derive the carpel from a glossopterid prototype (Fig. 4), since in glossopterids the cupules corresponding to the bitegmic ovules of angiosperms were attached to the middle, not the margins, of the subtending leaf.

Molecular data could also impinge upon neo-englerian scenarios by indicating whether or not conifers are related to angiosperms and *Gnetales*, but this would not be decisive, since the most parsimonious trees of Doyle & Donoghue (1992) included some in which conifers are the closest living relatives of anthophytes but Mesozoic seed ferns are interpolated between the two groups. The rRNA trees do not support a neo-englerian arrangement, since *Ginkgo*, cycads, and conifers form a clade, within which conifers are linked with cycads (Hamby & Zimmer 1992, Doyle & al. 1994). However, bootstrap analysis shows that the support for these relationships is weak.

In all these cases, present rRNA data must be considered inconclusive, since other molecular data sets have given different results, such as the basal position of *Ceratophyllum* in trees based on *rbc*L (Chase & al. 1993). A general problem is the fact that "long branches" on which there has been a large amount of molecular evolution tend to attract each other due to spurious convergences (Felsenstein 1978). It is possible that the basal position of *Ceratophyllum* in the *rbc*L analyses is due to this effect, since the position of *Ceratophyllum* in unrooted angiosperm trees is unstable (Qiu & al. 1993), suggesting a high level of homoplasy on the line leading to this genus. However, these conflicts may be resolved by study of additional sequences, recognition of rarer and thus potentially more reliable genome rearrangements (cf. Raubeson & Jansen 1992), or development of methods to correct for long branch attraction. For example, the fact that *Nymphaeales* remain basal in rRNA trees constructed using neighbor joining (Hamby & Zimmer 1992), a distance method that compensates to some extent for the problem of unequal branch lengths (Swofford & Olsen 1990, Huelsenbeck & Hillis 1993), is an argument against the view that the nymphaealean rooting found in the other rRNA analyses is due to long branch attraction.

A very different molecular approach might use genes involved in floral development as a key to morphological homologies in angiosperms and *Gnetales* (Doyle 1993). In the scheme of Coen & Meyerowitz (1991) and Bowman & al. (1991) for control of the identity of floral whorls in *Arabidopsis*, based on developmental mutants, the "A" genes specify perianth, while the "C" genes specify fertile parts. Activity of the "B" genes plus the "A" genes specifies petals as opposed to sepals, while activity of the "B" genes plus the "C" genes specifies stamens as opposed to carpels. A homologous system has been found in *Antirrhinum*, suggesting that it is general for eudicots, although evidence from magnoliids is needed before it can

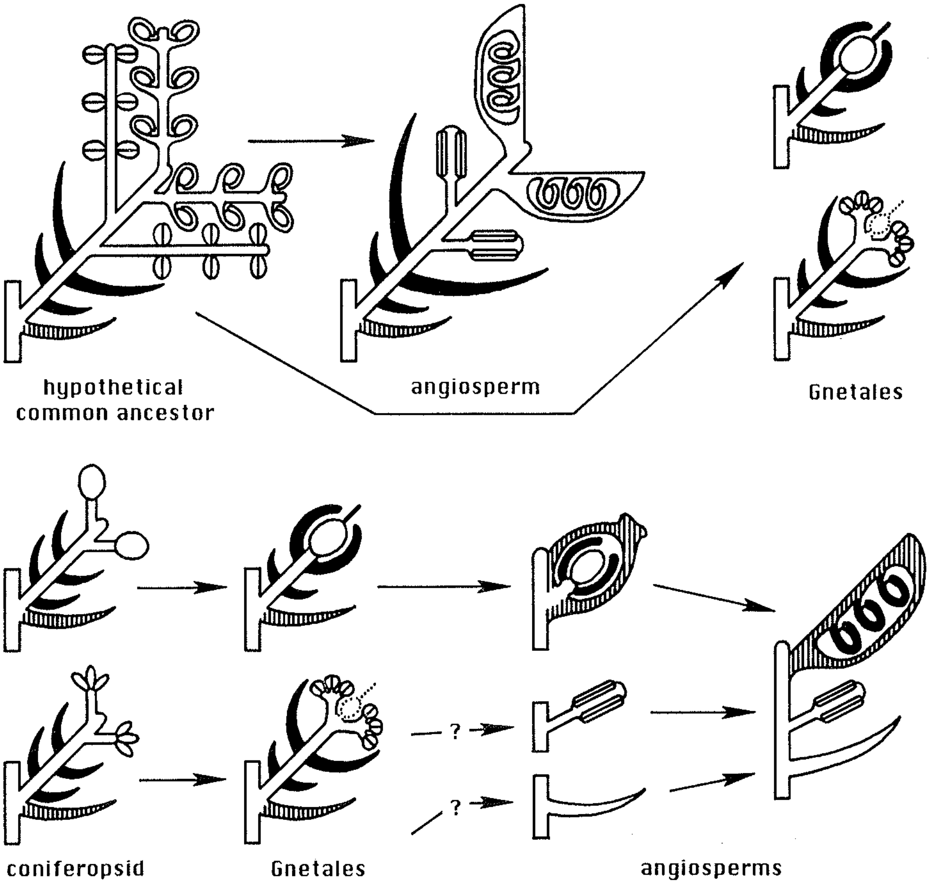

Fig. 6. Alternative homologies of angiosperm and gnetalean reproductive structures implied by a euanthial scenario (above), with anthophytes derived from a common ancestor with pinnately organized, cupulate megasporophylls, and a neo-englerian pseudanthial scenario (below), with flowers derived by aggregation of gnetalean units, emphasizing homologies of the gnetalean outer integument (black) and bract (hatched)

be assumed to be basic for angiosperms as a whole. In addition, ROBINSON-BEERS & al. (1992) have identified genes necessary for development of the integuments in *Arabidopsis*. To use such genes as evidence for the homology of structures in different groups, it will be necessary not only to identify the homologs of particular genes, but also to show that they are expressed in the putatively homologous structures.

It is easiest to see how this approach might distinguish between two extreme hypotheses (Fig. 6), the euanthial scenario of DOYLE & DONOGHUE (1986) and a neo-englerian pseudanthial scenario. The contrasting predictions may be seen by focusing on the outer integument of *Gnetales*. If the euanthial scenario is correct, the common ancestor of angiosperms and *Gnetales* had flowers with the standard order of parts, and it may be hypothesized that the system of floral genes and their present roles had arisen by this point. Therefore the outer integument of *Gnetales* would correspond to the perianth of angiosperms, and homologs of the "A" genes, such as *apetala 2* (COEN & MEYEROWITZ 1991), should be active during its development. In contrast, if the pseudanthial scenario is correct, the outer integument of *Gnetales* does not correspond to the angiosperm perianth, but rather to the angiosperm outer integument. Therefore homologs of the "A" genes should not be active during development of this layer in Gnetales, but rather homologs of genes required for development of the angiosperm outer integument. Looking further back, since the female "flower" of *Gnetales* would correspond to the ovuliferous cone scale of modern conifers, homologs of "outer integument genes" might also be involved in development of the conifer cone scale. Since the carpel wall would correspond to the subtending bract of *Gnetales* and conifers, homologous genes might be involved in the development of these structures.

How this scheme might relate to a polyphyletic origin of flowers within anthophytes (Fig. 4) is more ambiguous. Since the perianth would have arisen independently in angiosperms and *Gnetales*, development of the outer integument in *Gnetales* would not be expected to involve homologs of the "A" genes, but homologs of genes that specify the angiosperm outer integument should not be involved either. A developmental-genetic approach might also provide insights on other alternatives, such as MEYEN's (1988) gamoheterotopy hypothesis or the competing interpretations of the terminal ovule in the male flower of *Welwitschia*. In general, the relationships between genes and morphological homologies may be much more complex than those suggested here, due to duplications of genes and changes in their developmental roles. However, studies of this sort would be sure to add a new dimension to theories on the origin of the flower and its parts.

I am grateful to P. K. ENDRESS and E. M. FRIIS for their invitation to participate in this symposium, J. H. A. VAN KONIJNENBURG-VAN CITTERT for the opportunity to examine unpublished material of *Piroconites* and feedback on its interpretation, G. R. ROTHWELL for use of unpublished results on *Carnoconites*, K. R. ROBINSON-BEERS and C. S. GASSER for discussion of the genetics of floral development, and E. M. FRIIS and an anonymous reviewer for valuable comments on the manuscript.

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Accepted March 25, 1994 by E. M. FRIIS

Printed in Austria