# The origin and initial radiation of angiosperms in relation to anthophytes

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Autapomorphies indicate the angiosperms form a monophyletic group. Analysis of Aptian-Cenomanian macrofossils establishes that Chloranthaceae holds a central position in the initial radiation of dicots, while Palmae was basal to monocot initial radiation in the Maastrichtian. By tracing their fossil pollen back in time, two lines probably arose from two different species of *Monocrinopollis* (Crinopolles Group) in the Norian (Upper Triassic) The Crinopolles Group were extinct angiosperms that evolved directly from *Steevesipollenites* (Gnetales). The origin and initial radiation of angiosperms occurred in North America under stressful habitat conditions. Glossopteridales, Caytoniales and Bennettitales display extreme convergent tendencies to angiosperms, while Gnetales similarities to angiosperms are more numerous and fundamental. Gnetales-angiosperms and Bennettitales-Pentoxylales evolved as two distinct lines of anthophytes. Bennettitales arose from *Gangamopteris* (Glossopteridales) in the Lower Permian of South Africa, while Gnetales evolved either from Bennettitales or Glossopteridales at that time, also in South Africa.

## सारौंश

### परागकोशी पौधों से सम्बद्ध आवृतबीजीयों की उत्पत्ति एवं इनका प्रसार

#### ऑक्ले शील्ड

ओटापोमोर्फीय अध्ययन से प्रदर्शित होता है कि आवृतबीजी पौधे एक एकसंघीय समूह से सम्बद्ध हैं। ऍप्शियन-सीनोमानियन गुरुपादपाश्मों के विश्लेषण से यह प्रस्तावित होता है कि द्विबीजपत्रीयों के प्रारम्भिक विस्तार में क्लोरेन्थेसी की स्थिति केन्द्रीय है, जबकि मॉस्ट्रिक्शियन कल्प में एकबीजपत्री पौधों के विकीरण में पाल्मी कुल का आधारीय स्तर था। इन कुलों के अश्मित परागकणों के अभिलेखों से नारियन काल (उपरि त्रिसंघी) में **मोनोक्रीनोपॉलिस** (क्रीनोपॉलिस समूह) की दो विभिन्न जातियों से सम्भवतया दो दिशाओं में विकास हुआ है। क्रीनोपॉलिस समूह के पौधे विलुप्त आवृतबीजी थे जिनका विकास सीधे *स्टीवेसिपॉलिनाइटिस* (नीटेल्स) से हुआ है। आवृतबीजी पौधों की उत्पत्ति एवं इनका प्रारम्भिक विकीरण संघर्षमय परिस्थितियों में उत्तरी अमेरिका में हुआ था। ग्लॉसॉप्टेरिडेल्स, केटोनिएल्स एवं बेन्रीटाइटेल्स से सम्बद्ध पौधों में आवृतबीजी पौधों के प्रति केन्द्राभिसारी प्रवृत्तियां है जबकि नीटेल्स के पौधे आवृतबीजीयों से अधिक सजातीयता व्यक्त करते हैं। वास्तव में नीटेल्स-आवृतबीजी तथा बेन्रीटाइटेल्स-पेन्टॉक्सीलेल्स परागकोशी पौधों के दो विभिन्न समूहों में विकसित हुए है। बेन्रीटाइटेल्स की उत्पत्ति दक्षिण अफ्रीका में अधरि परमी कल्प में **गंगामॉप्टेरिस** (ग्लॉसॉप्टेरिडेल्स) से हुई है, जबकि उसी समय दक्षिण अफ्रीका में ही नीटेल्स का उद्भव बेन्रीटाइटेल्स अथवा ग्लॉसॉप्टेरिडेल्स से हुआ है।

IN recent years, studies in palaeobotany, palynology, cladistics, plant morphology, phytochemistry, and molecular sequencing have tried to solve the difficult problem of the origin of angiosperms. The early macrofossil and pollen records of angiosperms are reviewed here in order to document the origin and initial radiation of dicots and monocots, and the anthophyte groups are examined in some detail to determine which one was ancestral to angiosperms. The method used is the sequence of stratigraphic appearance of fossils, first as macrofossils and then (separately) as pollen, since angiosperms appear to have a fairly good fossil record. The angiosperms' place of origin, their monophyly, and their early adaptations to stressful habitats are also explored. For reviews of most of the numerous competing theories of the origin of angiosperms, see Pant and Kidwai (1971) and Stebbins (1974). The origins of Bennettitales and Gnetales are also given.

## ANGIOSPERM MONOPHYLY

There is an array of morphological, anatomical, embryological, palynological, and biochemical characters uniting most angiosperms that are lacking in other living spermatophytes (Ehrendorfer, 1977). These include pollenkitt, pollen walls generally tectate-columellate with non-laminated nexine, sieve tubes and companion cells

derived from the same mother cells, closed carpels with stigmatic pollen germination, stamens with two pairs of pollen sacs and an endothecial layer, triple fusion and endosperm development, and rRNA sequences with two-dozen shared advances (cf. Stewart, 1983, pp. 366-367; Dahlgren & Bremer, 1985; Donoghue & Doyle, 1989a, 1991; Troitsky et al., 1991). These autapomorphies strongly argue for a monophyletic, not polyphyletic, origin of angiosperms, although the monocot-dicot split must have occurred very early in their evolution. Recently it was demonstrated double fertilization, long considered a unique feature of angiosperms, occurs also in *Ephedra* (Friedman, 1990, 1992). Acceptance of angiosperm monophyly greatly simplifies the search for their point of origin among their Aptian-Cenomanian macrofossils.

## DICOT MACROFOSSILS

The earliest diversity of angiosperm macrofossils were all ancestral forms and were primarily Magnoliidae. Zone I (Aptian) Potomac Group leaves include *Eucalyptophyllum* (probably basal to Chloranthaceae and Illiciales), other leaves with ancestral (extinct) affinity to extant Chloranthaceae, and leaves having ancestral affinity to Illiciaceae and Schisandraceae (Upchurch, 1984a). Many Zone I leaves have disorganized, festooned brochidodromous venation found only in certain Magnoliidae families today (Hickey & Doyle, 1977). An unnamed plant with attached leaves and flowers from the Aptian of Victoria is probably basal to Chloranthaceae and Saururaceae (Taylor & Hickey, 1990), and a single androecium from the Upper Albian of Maryland is probably basal to Chloranthaceae (Friis et al., 1986; Crane et al., 1989). Other archaic forms of Magnoliidae include leaves reportedly close to Winteraceae and Himantandraceae from the Aptian of Virginia. *Archaeanthus* and *Lesqueria* from Upper Albian-Middle Cenomanian of Kansas (probably closely related to Magnoliaceae), and unnamed fruitification from the Turonian of Japan (probably basal to Austrobaileyaceae and Monimiaceae (cf. Wolfe, 1972; Dilcher & Crane, 1984; Crane & Dilcher, 1984; Nishida, 1985). "*Williamsonia*" *recentior* from the Lower Albian of Alberta occupies a basal relationship to *Archaeanthus* and *Lesqueria* (cf. Bell, 1956; Crane & Dilcher, 1984). Evidently, Chloranthaceae figured prominently in the initial radiation of Magnoliidae families in the Aptian and likely occupies the basal position in dicot phylogeny based on its fossil record (see Endress, 1987, p. 219). Leaves of the aquatic herb Nelumbonaceae first appeared in the Middle Albian of the Potomac Group, British Columbia, East Siberia, and Kazakhstan (Bell, 1956; Samylina, 1968; Doyle, 1973; Hickey & Doyle, 1977).

Leaves of apparently basal Hamamelidae are first known from the Aptian of Patagonia (Romero & Archangelsky, 1986). Some Albian Potomac Group leaves are similar to Platanaceae, with the first inflorescences of Platanaceae appearing in the Upper Albian of Maryland (Upchurch, 1984b; Friis & Crane, 1989). *Platanus*-like infructescences were found in the Late Albian-Cenomanian of Kansas and Wyoming (Dilcher, 1979; Crane, 1989, fig. 11). Platanoid leaves related to Platanaceae and Hamamelidaceae were the dominant foliar type in the Cenomanian of Alaska (Spicer et al., 1987). Leaves similar to Trochodendrales occurred in the mid-Late Albian of the Potomac Group (Crane, 1989).

Several of the earliest non-magnoliid flowers to appear were *Hyrcantha* from the Middle Albian of Kazakhstan (an archaic genus that was probably basal to Paeoniaceae and Ranunculaceae), and *Caspiocarpus* from the same beds (probably closest to Ranunculaceae) (Vachrameev & Krassilov, 1979; Krassilov et al., 1983). *Sapindopsis* leaves from the Albian of the Potomac Group are like Rosidae (Upchurch, 1984b). Diverse Rosidae leaves (*Sapindopsis, Celastrophyllum, Paliurus, Araliaephyllum*) with relatively well-preserved venation are reported from the Lower Albian of Alberta (Bell, 1956), and Icacinaceae wood is known from the Upper Albian of Utah (Thayn et al., 1985). The earliest Rosidae is *Sapindopsis* from the Lower Aptian of Alberta, and Late Albian *Sapindopsis* leaves have the most irregular tertiary venation of rosid fossils and thus the genus probably occupies the primitive base of Rosidae (cf. Bell, 1956; Upchurch & Dilcher, 1990). A generalized Rosidae flower was found in the Early Cenomanian of Nebraska (Basinger & Dilcher, 1984). According to Endress (1986, p. 5), "it looks most like certain Rosaceae, apart from the low stamen number." A primitive fruit of Rosaceae (*Asterocelastrus*) also occurs in the Cenomanian of Bohemia (Krassilov & Pacltova, 1989). The secondary chemistry of Dilleniidae-Rosidae is closest to Hamamelidae (Giannasi, 1986, table 7), and in combination with the known macrofossil record suggests that Dilleniidae-Rosidae evolved from lower Hamamelidae (see also Wolfe, 1989).

Unnamed elongate catkin inflorescences containing masses of *Retimonocolpites*-like pollen from the Lower Cenomanian of Kansas are probably closest to Chloranthaceae (Dilcher, 1979). Other fossils from the same beds with long infructescences include *Caloda* and *Prisca*. *Caloda* is perhaps ancestral to Platanaceae (Dilcher & Kovach, 1986). *Prisca* has fruitifications, follicles and bitegmic seeds that are similar to *Caspiocarpus* (Retallack & Dilcher, 1981a) and is perhaps ancestral to *Caspiocarpus*. Most likely the chloranthoid inflorescence, *Caloda,* and *Prisca* were Mid-Cretaceous survivors of an experimental line of Chloranthaceae

that has since become extinct which occupied a key position in dicot evolution.

During the Early to Middle Cenomanian of Kansas, early Magnoliidae and Rosidae were represented as brackish-water vegetation (Upchurch & Dilcher, 1990). The bulk of these were Magnoliidae or forms with a similar grade of leaf architecture. *Crassidenticulum* shows close similarities to extant Chloranthaceae. *Landonia* was probably basal to Monimiaceae and Gomoregaceae, confirming morphological evidence of their close relationship. *Cocculophyllum, Pabiana* and *Pandemophyllum* have strong similarities to Lauraceae. *Longstrethia* compares with extant Illiciales but has more poorly organized venation. The Rosidae (*Anisodromum* and *Citrophyllum*) show an advancement level comparable to other Early Cenomanian Rosidae.

## MONOCOT MACROFOSSILS

The earliest probable monocot macrofossils are herbaceous *Acaciaephyllum* leaves from the Barremian-Aptian Potomac Group, accompanied by generalized monocot pollen (especially *Liliacidites*) (cf. Doyle, 1973; Hickey & Doyle, 1977; Daghlian, 1981; Walker & Walker, 1984). Both are unassignable to family. In stark contrast with Aptian-Cenomanian dicots, the initial radiation of monocot macrofossils was delayed until Maastrichtian-Paleocene times, except for Palmae which first appear in the Coniacian of New Jersey and Gabon (Muller, 1979; Daghlian, 1981). There is, however, one detailed report of palmoid wood from the Upper Albian of Tunisia (Boureau, 1954). Palm pollen shows a major diversification during the Senonian, preceding that of all other monocot families, and thus supports morphological studies which suggest that palms are basal within the monocot clade (cf. Moore & Uhl, 1973; Muller, 1979). A zingiberaceous seed of an extinct genus is known from the Campanian of North Carolina (Friis & Crepet, 1987). The first diversification of primitive monocot families occurred in the Maastrichtian of North America, with Pandanaceae pollen from Montana and Wyoming, leaves similar to Smilacaceae and/or Dioscoreaceae from southeastern United States and leaves basal to Zingiberales from the western interior of North America (Daghlian, 1981; Jarzen, 1983). Also in the Maastrichtian, Musaceae fruits appeared in Deccan Intertrappean beds of India (Friis & Crepet, 1987). Reliable fossils attributed to the following monocot families first appeared in the Paleocene : Potamogetonaceae fruits from England, Restionaceae pollen from Texas and Hungary, Sparganiaceae fruits from North Dakota, Typhaceae pollen from Montana and Russia, and Araceae leaves from Kazakhstan (Daghlian, 1981). The claims of monocot macrofossils from the Barremian of Mongolia and South Primorye

and the Albian of the Kolyma Basin are instead gymnosperms (especially Gnetales) or are too poorly preserved to determine whether or not they were angiosperms (Friis & Crepet, 1987).

Monocots exhibit certain fundamental differences from dicots in their uniform sympodial growth form, dichotomous branching, lack of a cambium, fusion of cotyledons, constant stomatal-size, independent origin of vessels, duration of the mitotic cycle, and rRNA sequencing (Cheadle, 1953; Holttum, 1955; Dunn *et al.*, 1965; Greguss, 1968; Evans & Rees, 1971; Arnold *et al.*, 1988). Parsimony and compatibility analyses of rRNA sequences suggest that Magnoliidae and Liliaceae are the most primitive angiosperms (Troitsky *et al.*, 1991).

## FOSSIL POLLEN

Angiosperm pollen extends back into pre-Aptian times, i.e., prior to the first macrofossils. Chloranthaceae pollen displayed some diversification in the Aptian, with *Ascarina*-like pollen (*Clavatipollenites, Retimonocolpites*) in the Potomac Group, Central America, Argentina, the Falkland Plateau, Portugal, Germany, etc., and *Hedyosmum*-like pollen (*Asteropollis*) in the ?Barremian-Aptian of Transbaikalia and Mongolia. Winteraceae-like pollen (*Afropollis, Walkeripollis*) first appeared in the Late Barremian-Early Aptian of Israel and Gabon and the Aptian of Egypt, Israel, and the Potomac Group. The earliest-recorded Myristacaceae pollen is from the Middle Albian of Israel (Brenner & Crepet, 1987).

SEM and TEM have shown that the pollen of same Lower Cretaceous *Clavatipollenites* and extant *Ascarina* are practically identical (Walker & Walker, 1984; see also Kuprianova, 1967). During the Barremian, *Clavatipollenites* (sometimes with *Retimonocolpites*) had already become widespread, occurring in NE China, Queensland, Argentina, Patagonia, the Caribbean, Potomac Group, Gabon, Congo, offshore Morocco, Israel, and England (Doyle *et al.*, 1975, 1977; Brenner, 1976, 1987; Burger, 1981, 1990; Vakhrameyev, 1981; Gao, 1982; Hughes & Mc Dougall, 1987; Drinnan & Crane, 1990). *Clavatipollenites* is also known from the Hauterivian of England, the Valanginian of Italy, and the Upper Berriasian-Lower Valanginian of Spain (Barale *et al.*, 1984; Hughes & Mc Dougall, 1987; Ward *et al.*, 1989).

Liliaceae-like pollen (*Liliacidites, Stellatopollis*) is known from the Aptian of Gabon, Israel, and the Potomac Group. In the Barremian, *Liliacidites* (sometimes with *Stellatopollis*) was found in Argentina, Potomac Group, Gabon, Congo, offshore Morocco, Egypt, Israel, and England (Brenner, 1976; Doyle *et al.*, 1977; Burger, 1981; Vakhrameyev, 1981; Penny, 1986; Hughes & Mc Dougall, 1987; Drinnan & Crane, 1990). *Liliacidites* also

extended down to the Hauterivian of England and the Valanginian of Italy (Hughes & Mc Dougall, 1987; Ward *et al.*, 1989).

The monosulcate pollen type that is scattered within Magnoliidae and is dominant in monocots is restricted to these groups which are the most primitive angiosperms in pollen-based phylogenies (Nair, 1974; Walker, 1974, 1976a, b). The monosulcate type is also the earliest unequivocal angiosperm pollen to appear in the fossil record, during Hauterivian-Barremian times (Doyle, 1984; Crane *et al.*, 1989).

*Clavatipollenites* pollen has been found in association with fossil fruits of primitive, extinct Chloranthaceae in the mid-Cretaceous of North America (Doyle & Donoghue, 1993). Barremian *Clavatipollenites* from South America, Potomac Group, Africa and England have columellar structure typical of angiosperms or infratectal structure transitional between granular and columellar (Doyle *et al.*, 1975; Ward *et al.*, 1989). Some of the pollen assigned to *Clavatipollenites* from the Jurassic, however, have cycad-like alveolar exine structure; the shape of *Clavatipollenites* does superficially resemble cycads, especially in sulcus being rounded at its extremities, but it possesses tectate exine-like angiosperms (Kemp, 1968; Doyle *et al.*, 1975; Wolfe *et al.*, 1975). Other *Clavatipollenites* pollen reported from the Liassic of the North Sea Basin and the lowermost Jurassic of the Canadian Arctic should be examined for their exinal structure (Cornet, 1989a), although a solid, non-laminated endexine may be a better criterion since columellate exine is known to occur in scattered gymnosperms (Muller, 1984; Zavada, 1984; Vasanthy *et al.*, 1989; Burger, 1990). More difficult to simply dismiss is the report of *Liliacidites* and *Retimonocolpites* from the Norian of Pennsylvania (Cornet, 1989a). *Clavatipollenites* from the Lower Oxfordian of France does have a minute connate supratectal structure and so may be angiospermous (Cornet & Habib, 1992).

## TIME OF ORIGINATION

The monocot-dicot divergence likely occurred about 200-205 Ma (± 40 Ma), a minimum age estimate for angiosperms, based on chloroplast DNA sequence data, or 200-250 Ma based on nuclear rRNA genes (Wolfe *et al.*, 1989; Li *et al.*, 1989). Similarly, a monocot-dicot divergence date of about 205 Ma was obtained from partial protein sequences based on a much wider variety of angiosperms (Martin & Dowd, 1991). Most of these dates are within the range of the Norian (210-223 Ma) for the oldest purported angiosperm pollen of monocots and dicots cited here, and are within the range of the Carnian (223-235 Ma) for the Crinopolles Group pollen (see below). Other studies utilizing rRNA and the enzyme GAPDH obtain much older age estimates

of the Devonian-Carboniferous boundary and the Carboniferous, respectively (Martin *et al.*, 1989; Troitsky *et al.*, 1991), but these are not corroborated by the known fossil record and thus appear unlikely (Crane *et al.*, 1989). It is noteworthy that none of these molecular studies supports a Lower Cretaceous time of origination for angiosperms, when their initial radiation first occurred. The presence of the earliest-known mammal (*Adelobasileus*) and bird (*Protoavis*) in the Late Carnian and Early Norian, respectively, of Taxas (Chatterjee, 1991; Lucas & Luo, 1993), also suggests that angiosperms might have originated during the Upper Triassic (in North America) since birds and mammals today are major seed-dispersers of angiosperms (Regal, 1977), a symbiotic relationship.

## CLADISTICS AND ANTHOPHYTES

Cladograms utilizing large numbers of characters select Magnoliales *s. str.* as the basal angiosperms when anthophytes (other than angiosperms) plus *Caytonia* are the composite outgroup (Donoghue, 1989; Donoghue & Doyle, 1989b), yet the angiosperm macrofossil record indicates instead that Chloranthaceae is basal in dicots. Cladogram results are extremely sensitive to the first step of choosing an appropriate outgroup. Cladograms that incorporate most seed plant groups have demonstrated that anthophytes (angiosperms, Gnetales, Bennettitales, and Pentoxylales form the most advanced clade, which possess flower-like reproductive structure (Crane, 1985; Donoghue, 1989; Doyle & Donoghue, 1993), thus greatly narrowing the vast field of choices one is otherwise confronted with. Which one of these anthophyte groups represents the closest relative to angiosperms is problematic, however, with various cladograms indicating Bennettitales (Doyle & Donoghue, 1986a, b; Donoghue, 1989) or Pentoxylales (Doyle & Donoghue, 1992, 1993) but not Gnetales although they are the closest living relatives of angiosperms. Cladograms most often derive angiosperms from Bennettitales, sometimes Pentoxylales or Caytoniales, and occasionally Glossopteridales. It is also uncertain which anthophyte group is the most plesiomorphic. Though cladograms frequently show angiosperms as the basal clade of anthophytes, this is clearly incompatible with the fossil record of Gnetales. The fossil record for anthophytes is now fairly good, while cladistic analyses of anthophytes are still in an experimental stage.

There are several sources for potential error in these cladistic analyses. Bennettitales and Pentoxylales are extinct groups, while the Gnetales group invariably used comprises extant *Welwitschia*, *Ephedra*, and *Gnetum*. It would seem more appropriate to incorporate early fossil members of Gnetales instead when making cladistic comparisons, especially since extant members

have undergone reduction and specialization compared with Mesozoic fossils. Incorporating Caytoniales into the outgroup pool introduces another bias. The Caytoniales were all wind-pollinated, while wind-pollination in angiosperms is secondarily derived (Whitehead, 1969, 1983), although *Ascarina* and various palms are primitively anemophilous. The bisaccate, monosulcate pollen of Caytoniales have an alveolar wall structure that is not comparable with the tectate, atectate, or granular wall structure in primitive angiosperms (which, except for *Lactoris*, are non-saccate) and thus does not support a Caytoniales ancestry for angiosperms (Zavada & Crepet, 1986). Constructing a composite outgroup consisting of Gnetales, Bennettitales, Pentoxylales, and sometimes Caytoniales also introduces a bias into the resulting cladograms, rather than singling out one or trying each separately. In addition, missing characters provide a certain amount of leeway to the results, and extreme character convergence among anthophyte groups has the undesired effect of obscuring true relationships.

The Pentoxylales are not the closest ancestor to angiosperms. Meeuse's (1961) theory that Pandanaceae arose from Pentoxylales is not substantiated by their differences in reproductive structures, stem anatomy, leaf structure (particularly venation), and leaf shape (Stone, 1972; B.C. Stone, in litt.). The pollen of Pandanaceae is ornamented, unlike the smooth pollen surface of Pentoxylales, and extends back only to the Maastrichtian (cf. Vishnu-Mittre, 1953; Jarzen, 1983). The pollen, syndetocheilic leaf stomata, stomata orientation, and ovule structure of Pentoxylales are more similar to Bennettitales than they are to Cycadales (Rao, 1976; Frederiksen, 1980; Taylor, 1981), also supported by recent cladistic analyses (Crane, 1988). Thus the anthophyte group that is closest in relationship to angiosperms must either be Gnetales or Bennettitales.

Rooting angiosperms in paleoherbs involves one or two additional steps in the cladistic analysis (Donoghue & Doyle, 1989a) and would require that the angiosperms' closest outgroup was likely herbaceous. This appears doubtful since all known Gnetales, Bennettitales, Pentoxylales, Caytoniales, and Glossopteridales were woody, non-herbaceous plants.

Bennettitales-Pentoxylales and Gnetales-angiosperms are separate clades in Crane's (1985) cladogram. The Bennettitales share some characteristics with Gnetales in the seed, strobili, micropyle, stomata, vessels and an embryo "feeder" (Crane, 1988). In Gnetales, the embryo "feeder" is present in *Welwitschia* and *Gnetum* but is lacking in *Ephedra*. Cladograms that have angiosperms evolving directly from Bennettitales are likely in error. Bennettitales differ from angiosperms in ovules borne singly on stalks with ovules usually very numerous, ovules are enveloped by tightly-packed interseminal scales (unique to Bennettitales), the compound microsporophyll is not equivalent to angiosperm stamens, their cycad-like foliage differs from most all angiosperms, and their psilate pollen with laminated nexine is unlike the reticulate-columellar pollen with non-laminated nexine of pre-Aptian angiosperms. Delevoryas (1968) concluded that it is impossible to derive the flowers of angiosperms from Bennettitales because of their differing structural patterns, their resemblances being superficial. By the process of elimination, this leaves only Gnetales as the closest anthophyte group to angiosperms.

## GNETALES

Current opinion is divided between those who consider Gnetales similarities with angiosperms as convergent and those who consider Gnetales a direct link between gymnosperms and angiosperms. Both sides would agree, however, that Gnetales are unique among extant gymnosperms in possessing many angiosperm-like characters.

Some of the similarities are at a very fundamental level, as would be expected if their shared characters were inherited from a common ancestor. These include small chromosomes, extensive polyploidy and an original basic chromosome number of $X = 7$ (cf. Raven, 1975; Ehrendorfer, 1976). Double fertilization, a basic angiosperm trait, regularly occurs in *Ephedra nevadensis*, and double fertilization-like events have also been reported for *Welwitschia* and *Gnetum* (Friedman, 1990). In *Ephedra trifurca*, development of the second fertilization product is fundamentally similar to the endosperm of angiosperms, resulting in multiple embryos by nuclear proliferation rather than a specialized nonembryo tissue for the nourishment of the zygotic embryo (Friedman, 1992). Friedman hypothesizes that double fertilization is homologous in *Ephedra* and angiosperms, with *Ephedra* retaining the plesiomorphic reproductive character states of its common ancestor with angiosperms. *Ephedra* is also the only Gnetales with archegonia. In *Welwitschia* and *Gnetum* the female gametophyte is tetrasporic, but is monosporic in *Ephedra* and most angiosperms.

There are also some indications that Gnetales may have been the precursor to angiosperms. In angiosperms a pollenkitt is nearly universally present (even in anemophilous members) where it is an important component of the entomophily syndrome (Hesse, 1981, 1984). The Gnetales lack a pollenkitt, but *Ephedra* and *Welwitschia* possess sticky pollen. Insect pollination is widespread in angiosperms and Gnetales species are anemophilous or non-specialized entomophilous. The most plesiomorphic dicots and monocots (Chloranthaceae and Palmae, respectively) also both

contain anemophilous and entomophilous members (cf. Meeuse, 1972; Moore & Uhl, 1982; Endress, 1987). Reticulate early angiosperm pollen is more easily derived from striate Gnetales pollen than from psilate Bennettitales pollen. There is a great chemical structural similarity between the three Gnetales genera and the rosiflorean block of angiosperms, differing only in the substitution patterns of all phenolics (Gottlieb & Kubitzki, 1984). The similarity could be due to convergence or it might simply be a reversion pattern.

A comparison between Gnetales and angiosperms reveals other similarities. In *Ephedra* there are sometimes atavistic bisexual strobili, and there is a rudimentary ovule in male *Welwitschia*, suggesting their ancestors had bisexual strobili. Most angiosperms have bisexual strobili. Pollen tubes of male gametophyte development are unbranched in Gnetales and many angiosperms. Gnetales pollen has granular exine as in some primitive angiosperms. The stem apices of *Ephedra* and *Gnetum* have a double-layered cellular arrangement, with the outer tunica layer as in angiosperms. *Welwitschia* and *Gnetum* leaves have vein anastomoses and tertiary veining as in angiosperms. Gnetales and angiosperms possess bitegmic ovules. Vessels are dominant in angiosperms, and the lack of vessels within some primitive angiosperms has been shown cladistically to be secondarily derived (Young, 1981). All Gnetales possess vessels in their secondary wood, with circular bordered pits in *Welwitschia* and *Ephedra* but with scalariform tracheids in *Gnetum* as in any primitive angiosperms (see Muhammad & Sattler, 1982). The wood of *Ephedra* has a multiseriate ray structure as in primitive dicots. Gnetales bracteoles may be comparable to a secondary integument in angiosperms. Both *Welwitschia* and monocot trees exhibit dichotomous branching, with paedomorphism present in *Welwitschia* and monocots. The syndetocheilic stomata of *Welwitschia* and some *Gnetum* and the haplocheilic stomata of *Ephedra* and some *Gnetum* resemble the stomata of many angiosperms. *Ephedra* is similar to some monocots in having regular rows of uniform epidermal cells in the stem and leaf, and surface papillae on the leaves (Pant & Verma, 1974). Casuarinaceae and some *Eriogonum* species (e.g. *E. smithii*, *E. ephedroides*) are reminiscent of *Ephedra* in growth form.

It appears unlikely that the various Gnetales-angiosperm similarities are due to convergence since these are often widespread and sometimes fundamental, and definite obstructing characters have not been found. In contrast, the similarities between Caytoniales-Chloranthaceae, Bennettitales-Magnoliaceae, and Pentoxylales-Pandanaceae are not usually so widespread within angiosperms and are more likely due to convergence because of certain obstructing characters. Since Gnetales pollen preceeds angiosperm pollen by

about 65 Ma in the fossil record, they would be the more plesiomorphic of the two and not the reverse that is most often shown in cladograms.

In extant Gnetales, *Welwitschia* (1 sp.) is found in coastal deserts of South West Africa, *Ephedra* (ca. 40 sp.) are xerophytic shrubs (sometimes trees and vines) in arid to semi-arid regions of the world, and *Gnetum* (ca. 35 sp.) are climbers (sometimes trees) mainly in trans-tropical rainforests.

## *DREWRIA* AND *SANMIGUELIA*

*Drewria* from the Aptian of Virginia is gnetalean since its leaf venation is like that found in *Welwitschia* cotyledons, opposite bracts surround the seeds, there is a network of subepidermal foliar fibers, and the pollen is polyplicate (Crane & Upchurch, 1987). *Drewria* also displays similarities to Chloranthaceae in its opposite and decussate leaves borne at swollen nodes, dichasially arranged inflorescences that are spike-like, and reproductive structures that are surrounded by pairs of bracts, although extant Chloranthaceae differ from *Drewria* in possessing toothed leaves, a midrib with pinnate secondary veins, and lack of a network of subepidermal fibers.

*Sanmiguelia* first appeared in the Early Carnian of Virginia and was present in the latest Carnian of Colorado, the lowermost Norian of Texas, the Early or Middle Norian of Utah, and the Hettangian of Arizona (Cornet, 1989b; Shields, 1992, 1993). Until recently it was variously placed in Palmae (near *Paloreodoxites),* near *Veratrum* (Liliaceae), or even in Bennettitales, Cycadaceae, or *Schizoneura* (cf. Brown, 1956; Arnold, 1963; Becker, 1964, 1971, 1972; Read & Hickey, 1972; Tidwell *et al.*, 1977). Cornet (1986, 1989b) uncovered much more complete fossil material of *Sanmiguelia* in the Trujillo Formation of western Taxas, thus allowing him to make a better assessment of its systematic position.

The secondary wood and flowers of *Sanmiguelia* are homologous with Gnetales. However, it may be a very primitive angiosperm that displays dicot and monocot characters in combinations that are no longer found in either and thus may be very close to the early evolutionary link between dicots and monocots. Angiosperm-like characters include paired and biloculate anther-like sporophylls, reticulate leaf venation, tectate-granular pollen that is psilate monosulcate, and carples each bearing two anatropous ovules (Crane, 1987). General dicot characters possessed by *Sanmiguelia* include the presence of secondary xylem, cambium, primary tap root and an embryo with two large cotyledons (though one was significantly larger than the other). *Sanmiguelia* shares characteristics with various Chloranthaceae in rhizotomous habit, vesselless secondary xylem of restricted development in the lower

part of the stem, vessels in the secondary xylem of roots, unisexual reproductive structures that are dimorphic, ovules with a prominent inner integument projecting well beyond the outer integument, and variable orientation of carpels. *Sanmiguelia* also shares characteristics that are scattered within monocots, such as male and female inflorescences comparing more favorably with monocots than dicots (e.g. female inflorescence resembles extant *Yucca* or *Lilium*, male inflorescence resembles Araceae such as *Arisaema*), and its venation is poorly organized as in some Araceae seedlings. In Cornet's view, *Sanmiguelia* is more closely related to angiosperms than to any other group of seed plants.

## CRINOPOLLES GROUP

Cornet (1989a) interpreted Crinopolles Group of pollen from the Early Carnian to late Middle Carnian of Richmond Basin, Virginia, as angiospermoid, occupying the morphological gap between dicots and monocots. The pollen has reticulate-columellate-footlayer, ectexinal and non-laminated endexinal structure, features usually considered angiosperm autapomorphies, and thus "may represent the oldest clues to the origin and early evolution of the angiosperms." These crinopolles-angiosperm features are unknown in fossil and extant gymnospermous pollen.

As originally conceived, the Crinopolles Group contained 7 genera, but *Placopollis* should be excluded because it has endexine laminations, as should *Steevesipollenites hemiplicatus* since other *Steevesipollenites* species clearly belong in Gnetales. The five remaining Crinopolles Group members include *Pentecrinopollis* (2 sp., Early Carnian), *Tricrinopollis* (2 sp., Early Carnian), *Monocrinopollis* (4 sp., Early to Late Carnian), *Dicrinopollis* (1 sp., Early Carnian), and *Zonacrinopollis* (1 sp., Early Carnian). Cornet suggests that *Steevesipollenites hemiplicatus* (Early Carnian) occupies an intermediate position between *Pentecrinopollis* and normal *Steevesipollenites* in relationship. The group underwent rapid diversification in geographic isolation during the Early Carnian. The parent plants have not been discovered, with the possible exception of one leaf (see below).

With *Steevesipollenites* as the precursor to the Crinopolles Group, Cornet prefers an interpretation that pentasulcates were basic, with monosulcate morphotypes (*Monocrinopollis*) the most derived in the series. *Monocrinopollis* consists of Early to Middle Carnian *M. doylei, M. mulleri* and *M. walkeri* and Early to Late Carnian *M. microreticulatus* and *M. walkeri* range the highest stratigraphically, becoming the most common crinopolles in the Richmond and Taylorsville basins. *M. microreticulatus* was only crinopolles member to

range outside of the group's center, being present in the Middle Carnian of North Carolina and the Late Carnian in northeastern Arizona. He considers *Retimonocolpites* and *Liliacidites* from the Norian Newark Basin of Pennsylvania as indicating continued survival of the Crinopolles Group since they closely resemble *Monocrinopollis* except for lacking an endexine and footlayer (by probable reduction).

Cornet (1989a) noted general similarities between the Crinopolles Group and monocots, many of these taxa having a dimorphic exine structure as in monocots, with the absence of a distal footlayer and the presence of an endexine preventing him from classifying crinopolles as monocot pollen (Cornet & Olsen, 1990), although they could represent a line of angiosperms in the Upper Triassic that is more primitive than extant angiosperms (Doyle & Hotton, 1991). A comparison between the most angiosperm-like crinopolles (*Monocrinopollis*) and the earliest undoubted angiosperm pollen (*Clavatipollenites, Retimonocolpites, Liliacidites*) better resolves their relationships (cf. Doyle *et al.*, 1975; Walker & Walker, 1984; Zavada, 1984; Cornet, 1989a). All are reticulate-columellate monosulcates. The exine has a footlayer present in *Monocrinopollis* and *Clavatipollenites*. The endexine is non-laminated and is thick under the distal aperture in *Monocrinopollis* and *Clavatipollenites bughesii* (the nexine is thin in *Liliacidites* but occasionally thick under the distal aperture). *Monocrinopollis mulleri, Clavatipollenites,* and *Retimonocolpites* have a similar reticulate network. *Monocrinopollis walkeri* and *Liliacidites* have strongly dimorphic lumina in the tectum. A psilate tectum with round lumina is present in *Monocrinopollis microreticulatus* and *Liliacidites,* and semitectate exine occurs in *Monocrinopollis mulleri, Retimonocolpites* and Norian *Liliacidites. Monocrinopollis* (usually) and *Retimonocolpites* have elliptical pollen, while spherical pollen is found in *Monocrinopollis* (some), *Clavatipollenites,* and some *Liliacidites.* An average size range of ca. 20-30 μm occurs in *Clavatipollenites, Retimonocolpites, Liliacidites* and *Monocrinopollis microreticulatus.* Thus *Monocrinopollis* actually shares the largest number of internal and external pollen morphological features with *Clavatipollenites. Monocrinopollis* species exhibiting the most similarity with these particular angiosperms are *M. mulleri* and *M. microreticulatus,* the only Crinopolles Group survivors in the Middle Carnian. The other Crinopolles Group genera show fewer similarities. The results suggest that *Monocrinopollis* was the ancestral genus that gave rise to both dicots and monocots and that the earliest dicot may have slightly preceded the earliest monocot, from *M. mulleri* and *M. microreticulatus,* respectively. Found in fairly close association with *Monocrinopollis microreticulatus* was a dicot-like leaf being described

by Cornet (pers. comm.; see also Cornet & Habib, 1992, Addendum), from the Late Carnian of North Carolina, which is proto-*Ascarina* in my opinion

*Steevesipollenites* is known from the Upper Permian of Oklahoma, the Middle Triassic of Argentina, and the Early Carnian of Virginia, then, following a hiatus in the Jurassics ranges in the Aptian-Albian of northeast Brazil and the Falkland Islands offshore, the Albian and Cenomanian of northeast Peru, and the Albian-Turonian of Senegal Basin in West Africa (Stover, 1964; Brenner, 1968; Herngreen & Chlonova, 1981; Cornet, 1989a; Osborn *et al.*, 1993). A precursor to *Steevesipollenites* may have been *Tornopollenites* from the Lower Permian of Texas (see Morgan, 1971).

Gnetales may have arisen from Glossopteridales of the Southern Hemisphere as suggested by their striate pollen, but macrofossil connections are unknown or at least unrecognized. Apparently the only Gnetales pollen from the Lower Permian of the Southern Hemisphere were four species of *Gnetaceaepollenites* from South Africa (Anderson, 1977). One of these (*G. sinuosus*) extended to Upper Permian times is South Africa, India, New South Wales, etc., and is said to be widely occurring then excepting South America (cf Balme & Hennelly, 1956; Bharadwaj, 1963; Anderson, 1977). *Pentecrinopollis traversei* of crinopolles is strongly reminiscent of *Gnetaceaepollenites bulbiger* from the South African Lower Permian in the exine bearing numerous large, prominent clavae, a unique parallelism or reversal suggestive of a possible distant relationship.

## EARLY COLONIZATION

During the Lower Permian in South Africa, *Gnetaceaepollenites* occupied delta-front, delta, fluviatile and coal swamp deposits.

The Crinopolles Group rapidly diversified in the Early Carnian under arid conditions, with *Steevesipollenites hemiplicatus* itself preferring fluvial, delta and levee environments. During the Middle and Late Carnian, climates changed to seasonal monsoons and large lakes and swamps developed. *Monocrinopollis mulleri* occupied delta top and levee environments and unstable shorelines of large lakes, and *M. microreticulatus* preferred fluvial over bank, deltas and levee environments and was probably an opportunist. Climatic extremes and population fluctuations likely pre-adapted them to survive in low numbers and to rapidly colonize new areas (Cornet, 1989a; Cornet & Olsen, 1990). *Sanmiguelia* preferred sites that bordered a meandering river channel subject to periodic flooding and at the edge to an interdistributary lake or pond (Cornet, 1986). DiMichele *et al.* (1987) observe that these are intrinsically stressful habitats where macroevolutionary changes have a greater likelihood

of surviving due to low competition, there being strong selection pressures against plants that are intolerant of the stress agents (such as periodic flooding). These sorts of habitats were spatially disjunct such that migration opportunities were limited. Marine organisms similarly produce higher rates of evolutionary novelties in stressful near-shore environments where species diversity is low (Lewin, 1983).

During the initial radiation of dicots in Aptian-Cenomanian times, there was widespread dispersal of pioneering coastal angiosperms coinciding with maximum oscillations of epicontinental seaways, spawning the coastal hypothesis for the dispersal and rise to dominance of angiosperms (Retallack & Dilcher, 1981b, 1986). These were ecologically opportunistic plants with preadapted ability to colonise disturbed sedimentary surfaces. By Albian-Cenomanian times, these dicots occupied a number of different habitats, including coastal lagoons, coastal streams, river levees, deltas, swamps, lake margins, and floodplains, while conifers remained dominant in more well-drained inland soils. These environments are remarkably similar to the ones occupied by their Carnian ancestors.

The Carnian Crinopolles Group pollen, the Aptian early dicot macrofossils and the Maastrichtian early monocot macrofossils all show a pattern of initial radiation in North America, suggesting this continent was their place of origin. There were extensive migrations of a few early angiosperm pollen taxa outside of North America during the Lower Cretaceous, but they were at a much lower level of diversity. Albian angiosperm leaves from Portugal and Russia were fairly diverse and plesiomorphic, but Russian Aptian fossils do not indicate that an initial radiation occurred there (cf. Samylina, 1968; Hughes, 1976. pp. 134-142).

Today *Ascarina* (11 sp.) is found primarily in tropical rainforest habitats and is distributed in the Philippines (Luzon, Panay, Mindanao), northern Borneo, Celebes, New Guinea, New Britain, Manus Island, Solomons, New Hebrides, New Caledonia, New Zealand, Kermadecs, Samoa, Fiji, Cooks (Rarotonga), Society Islands (Tahiti, Raiatea) and the Marquesas (Nuku Hiva) (Swamy, 1953; Smith, 1976; Verdcourt, 1986). *Clavatipollenites* pollen first entered this region during the Upper Barremian in Queensland (Burger, 1990). The most primitive extant palms reside in South America, with related genera in southeastern United States, Europe, and southeastern Asia (Moore & Uhl, 1982).

## ACANTHACEAE

The exterior surfaces of *Cornetipollis* (from the Carnian of Virginia, New Mexico, Arizona and northwest Australia) and certain Acanthaceae genera bear a strong resemblance in their pollen banding patterns (cf. Pocock

& Vasanthy, 1988; Cornet & Habib, 1992). However, these differ in columellar shape and orientation, the colporate apertures in Acanthaceae are lacking in *Cornetipollis,* and columellae are fused to the underlying nexine in *Cornetipollis* but not in *Bravaisia* (Pocock & Vasanthy, 1988). Thus their similarities appear to be superficial and are more likely due to convergence than homology. Columellate exine is also present in *Equisetosporites* and *Ephedripites* (which, however, have laminated endexine or nexine) and so is not an exclusively angiospermous character. Acanthaceae is a member of the highly-evolved Asteridae, which in turn has connecting links to Rosidae (Takhtajan, 1969). Any Acanthaceae connection with Gnetales would necessitate that dicots are paraphyletic and Asteridae is unrelated to Rosidae, viewpoints unsupported by various neontological studies. *Cornetipollis* is frequently considered to have evolved directly from *Equisetosporites* and the Late Carnian Arizonan plant that bore *Equisetosporites* pollen (*Dechellyia* leaves, *Masculostrobus* infructescences) does not even slightly resemble Acanthaceae (see Ash, 1972).

Cornet and Habib (1992) note that *Multimarginatus* from the Lower Oxfordian of France compares most closely with extant *Sanchezia* and *Bravaisia* in overall shape, size, wall structure and apertures. The fact that *Multimarginatus* pollen and *Stellatopollis* grains from that same sample corresponding so closely with extant relatives strongly suggests contamination. Though they were careful to take the proper precautions, this possibility cannot be ruled out since these grains did not survive on mounts for a few years, with some surviving grains becoming enlarged and more translucent while other taxa from the same strata did survive intact.

## BENNETTITALES

During the Upper Triassic, many genera of Bennettitales first radiated in the Northern Hemisphere and occupied southern North America, Greenland, Sweden, Austria, Switzerland, Iran, South China, Japan, and Siberia. Bennettitales pollen is primarily psilate monosulcate and thus is not readily distinguishable from certain other gymnosperms, although *Norian Bennettiteaepollenites* was striate (see Staplin *et al.*, 1967). The earliest unequivocal Bennettitales fossils were *Williamsonia* and *Otozamites* from the Carnian and Middle Triassic of Queensland (Jones & de Jersey, 1947; David, 1950), and *Williamsonia* stems have been reported from Late Scythian to Early Anisian (uppermost Lower Triassic to lowermost Middle Triassic) in New South Wales (Retallack, 1975). *Zamites,* too, is recorded from the Ladinian (upper Middle Triassic) of Germany (Mader, 1990). There are a few Lower Permian plants from South Africa that could well be ancestral

Bennettitales, but their preservation is insufficient to establish the relationship with absolute certainty. These include *Plumsteadiella, Lerouxia* and *Vannus* which have stalked or attached fruitifications, strongly reminiscent of Bennettitales, especially *Williamsonia* and *Williamsoniella* (Plumstead, 1961, 1963; Le Roux, 1966). *Plumsteadiella* occurred in association with a *Gangamopteris* sp. leaf, and *Vannus* was found in an axillary position of growth on a *Gangamopteris* cf. *Clarkeana* leaf. If these were ancestral Bennettitales, they would support the anthophyte-Glossopteridales link found by cladistics.

The possibility that Bennettitales arose from Gnetales appears excluded by these fossils, although Gnetales might have arisen from Bennettitales as suggested by Takhtajan (1958) based on bisexual strobili considerations. Currently the fossil information is inadequate to determine whether Gnetales arose from Bennettitales or Glossopteridales. It would help to know what the plants looked like that produced *Gnetaceaepollenites* and what sort of pollen was produced by the Bennettitales in the Lower Permian of South Africa.

## ACKNOWLEDGEMENTS

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