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Paleobotanical evidence on the early radiation of nonmagnoliid dicotyledons

PETER R. CRANE

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Abstract: Paleobotanical studies indicate that several isolated and systematically depauperate groups of extant woody dicotyledons originated in the Mid Cretaceous. The *Chloranthaceae* had probably differentiated into insect-pollinated (*Chloranthus* and *Sarcandra*) and wind-pollinated (*Ascarina* and *Hedyosmum*) forms by the end of the Albian, and leaves referable to the *Trochodendrales* are known from the Albian and Cenomanian. In the latest Cretaceous and Early Tertiary, extinct representatives of the *Trochodendrales* included *Nordenskioldia* and the *Joffrea-Nyssidium* complex. The *Platanaceae* also differentiated before the end of the Albian and initially had insect-pollinated, unisexual flowers with five carpels or stamens. Some of these features persisted in the platanoid lineage until the Early Tertiary, and during the Paleocene and Eocene the *Platanaceae* included forms with elliptical, palmate and pinnate foliage. The history of the *Platanaceae* suggests that several features of the reproductive morphology of extant taxa may have arisen in association with a trend toward wind pollination. In the Mid Cretaceous, platanoid foliage partially intergrades with pinnate *Sapindopsis* and pedate *Debeya-Dewalquea* leaves suggesting a close relationship between *Platanaceae* and *Rosidae* and *Fagaceae* respectively. The *Chloranthaceae*, *Trochodendrales*, and *Platanaceae* all occupy a somewhat intermediate position between the *Magnoliidae* and *Hamamelidae* and are of considerable interest with respect to their role in the initial radiation of nonmagnoliid ("higher") dicotyledons.

In the last three decades paleobotanical investigations have clarified the timing and pattern of early angiosperm evolution, and have identified the Mid Cretaceous as the interval during which the group underwent major diversification. Although it is possible that the angiosperm lineage diverged from related gymnosperm groups as early as the Triassic (CRANE 1985, DOYLE & DONOGHUE 1986) current knowledge of Mesozoic floras makes it unlikely that the angiosperms were diverse or abundant prior to the Cretaceous. The earliest unequivocal angiosperm pollen is reported from the Hauterivian (BRENNER 1984, HUGHES & MCDOUGALL 1987), and through the Hauterivian to Cenomanian interval (approx. 131 – 91 myr B.P.) angiosperm leaves, pollen and other reproductive structures increase dramatically in their variety and abundance in fossil floras (BRENNER 1963, DOYLE 1969, MULLER 1970, DOYLE & HICKEY 1976, HICKEY & DOYLE 1977, CRANE 1987, FRIIS & CREPET 1987). This

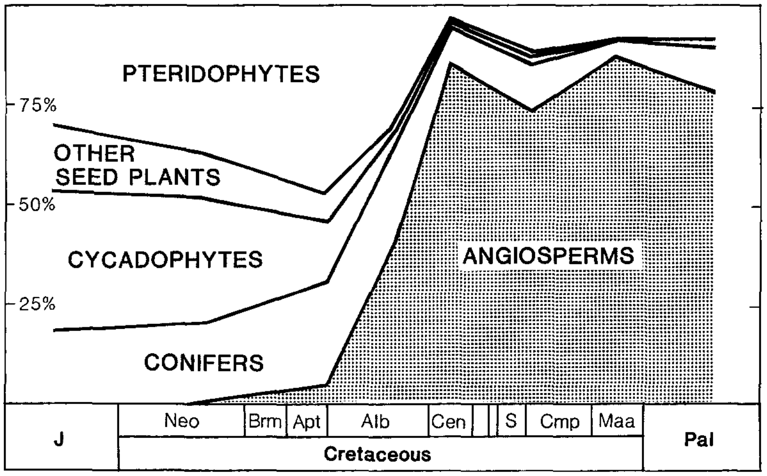

Fig. 1. Floristic change through the Cretaceous. Based on mean species number (expressed as a percentage) in 70 Jurassic, Cretaceous and Paleocene floras. Similar patterns are obtained using mean genus number (expressed as a percentage), or genus or species number without conversion into percentages. Cycadophytes includes *Bennettitales* and true cycads. See CRANE (1987) for lists of data and full explanation. J Jurassic; Neo Neocomian; Brm Barremian; Apt Aptian; Alb Albian; Cen Cenomanian; S Santonian; Cmp Campanian; Maa Maastrichtian; Pal Paleocene

clear chronological pattern is thought to reflect a major ecological and systematic radiation of flowering plants (DOYLE & HICKEY 1976, HICKEY & DOYLE 1977) that correlates with the decline of many gymnosperm and pteridophyte groups (Fig. 1) (CRANE 1987). During this interval many of the features characteristic of extant angiosperms appear for the first time (Fig. 2) and by the early Cenomanian at least three of the six dicotyledonous subclasses (*Magnoliidae, Hamamelidae, Rosidae*) were well established (WOLFE & al. 1975, DOYLE & HICKEY 1976, HICKEY & DOYLE 1977). Paleobotanical work is now clarifying the relationships of the fossil groups involved in the Mid Cretaceous angiosperm radiation and has demonstrated that the lineages clearly leading to several groups of extant woody dicotyledons had already diverged at a very early stage. In this paper I briefly review the fossil history of three of these groups, the *Chloranthaceae*, *Platanaceae* and *Trochodendrales*, in the context of the initial radiation of nonmagnoliid dicotyledons.

The **provenance of specimens** illustrated is as follows: BM, British Museum (Natural History), herbarium; British Museum (Natural History), paleobotanical collections; F, Field Museum of Natural History, herbarium; IU, Indiana University, paleobotanical collection; PP, Field Museum of Natural History, paleobotanical collections; UCMP, University of California, Berkeley, Museum of Paleontology; USNM, U.S. National Museum, Washington, D.C.

Chloranthaceae

The *Chloranthaceae* include the extant genera *Ascarina, Chloranthus, Hedyosmum,* and *Sarcandra,* and have attracted attention because of their simple floral structure and the absence of vessels in the secondary xylem of *Sarcandra* (SWAMY 1953,

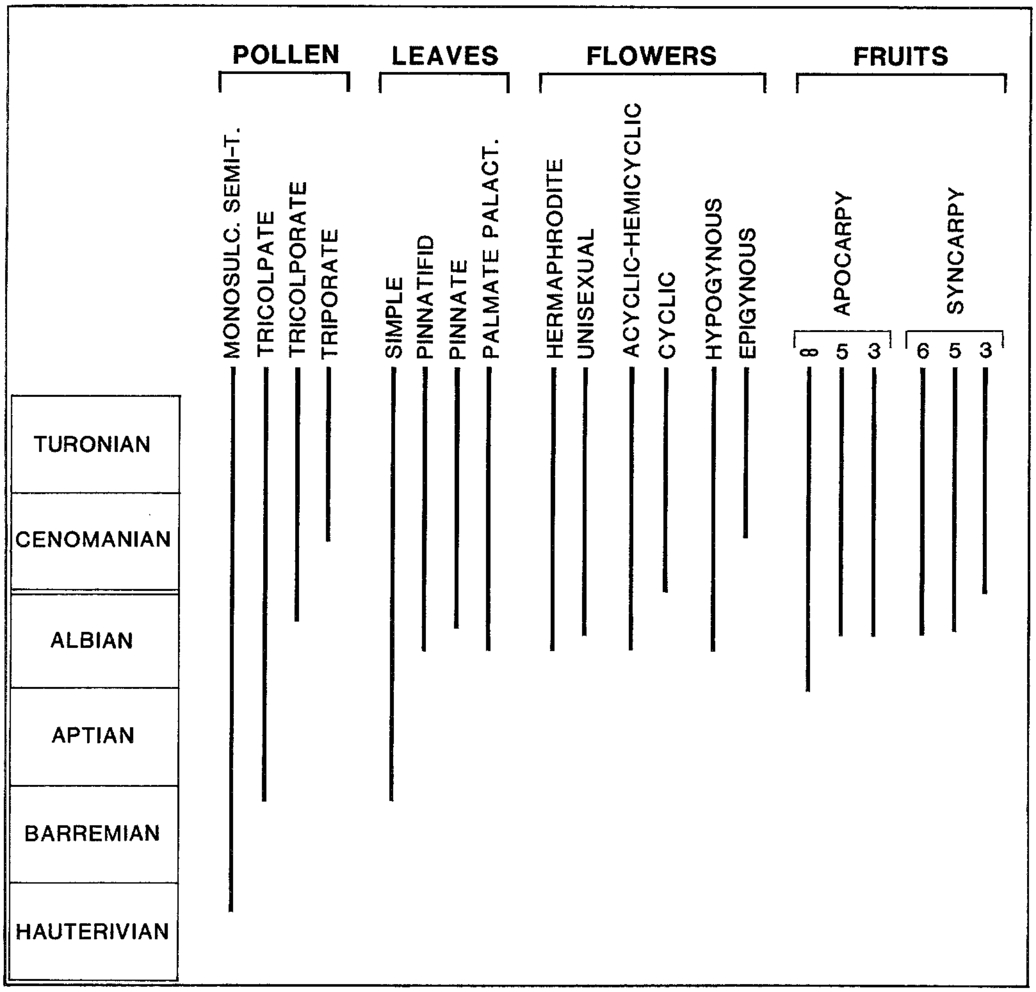

Fig. 2. Appearance of major angiosperm pollen, leaf, flower and fruit characters through the mid-Cretaceous. Monosulc. Semi-T, monosulcate semitectate; Palact, palinactinodromous. Based on Doyle (1978), Doyle & Hickey (1976), Brenner (1984), Friis & Crepet (1987), Crane (1987), Hughes & McDougall (1987). Note that monosulcate semi-tectate pollen occurs as early as the Triassic (Cornet 1979) but the relationships of these grains are currently uncertain

Swamy & Bailey 1950, Endress 1987 b). *Chloranthus* and *Sarcandra* have bisexual flowers, brightly colored androecia, small stigmatic surfaces and small anther thecae relative to the size of the staminal filament. All of these features are apparently associated with an entomophilous pollination syndrome (Endress 1986 b, 1987 b). *Ascarina* and *Hedyosmum* have inconspicuous unisexual flowers with large dry papillose stigmas apparently associated with an anemophilous pollination syndrome (Endress 1987 b). Together with disintegration of the innermost layers of the ovary wall at anthesis, and the presence of slime cells (Endress 1987 b), these features may be synapomorphies in the context of the *Magnoliidae* as a whole. Present knowledge therefore suggests that *Ascarina* and *Hedyosmum* together form a clade, but whether *Chloranthus* and *Sarcandra* form a monophyletic group is less certain

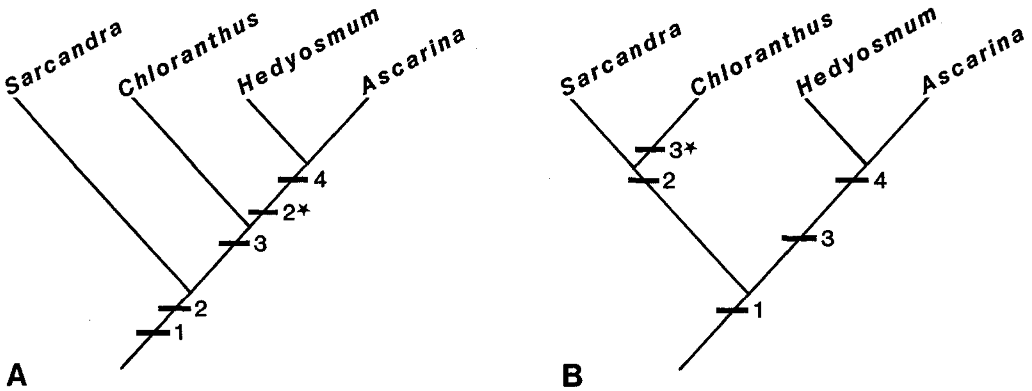

Fig. 3. Alternative hypotheses of relationships in extant *Chloranthaceae*. 1 Chloranthaceous synapomorphies, e.g., flowers lacking a perianth (except possibly *Hedyosmum*, see Endress 1987b), unicarpellate gynoecium with a single pendent orthotropous ovule (Endress 1987b), stamens anterior with respect to gynoecium (Endress 1987b); 2 swollen, brightly colored androecia and other characters apparently associated with entomophilous pollination (Endress 1987b); 3 vessels; 4 synapomorphies of *Ascarina* and *Hedyosmum*, e.g., unisexual flowers, disintegration of the inner ovary wall, presence of slime cells (Endress 1987b). *A* Single origin of vessels (3) requires either loss of entomophilous pollination syndrome (as shown, 2 and 2*) or independent acquisition of these features in *Chloranthus* and *Sarcandra*; *B* single origin of the entomophilous pollination syndrome (2) and monophyly of *Chloranthus*, *Sarcandra* clade requires double origin of vessels (as shown, 3 and 3*) or loss of vessels in *Sarcandra* (e.g., Young 1981)

(Fig. 3). If vessels evolved only once within the family then *Chloranthus* would be resolved as more closely related to *Ascarina* and *Hedyosmum* (Fig. 3 A).

Systematically, the *Chloranthaceae* are included within the *Magnoliidae* but similarities to certain *Hamamelidae*, particularly the *Trochodendrales* (simple sometimes unisexual flowers, chloranthoid leaf teeth, absence of vessels in *Sarcandra, Tetracentron, Trochodendron*), have led to the suggestion that the group occupies an intermediate position between these two subclasses (Walker & Walker 1984, Endress 1987b). Walker & Walker (1984) included the family in their *Piperiflorae* with the *Lactoridaceae, Piperaceae* and *Saururaceae*. The *Piperaceae* and *Saururaceae* were interpreted as more closely related to each other than either is to the *Lactoridaceae*; and the *Chloranthaceae* were interpreted as the sister group to the other three families. Endress (1987b) also acknowledged resemblances to the *Piperales* but placed the family in the *Laurales* based on similarities to the *Trimeniaceae* and *Amborellaceae*.

Paleobotanically the *Chloranthaceae* first attracted attention because of similarities between pollen of extant *Ascarina* and the fossil grain *Clavatipollenites hughesii* Couper, which is widespread in the Mid Cretaceous (Couper 1958, Kuprianova 1967, Doyle 1969, Muller 1981, 1984). Detailed S.E.M. and T.E.M. investigations of early angiosperm pollen grains have corroborated these observations and demonstrated strong similarities between *Clavatipollenites* and *Ascarina*, and between the fossil grain *Asteropollis* and pollen of *Hedyosmum* (Walker & Walker 1984). Other fossil grains (*Stephanocolpites*) have been compared with those of extant *Chloranthus* (Walker & Walker 1984). Studies of Cretaceous angiosperm reproductive structures have also yielded well preserved chloranthoid androecia from the Upper Albian of eastern North America and the Upper Santonian/Lower Campanian of southern Sweden (FRIIS 1985, FRIIS & al., 1986, CRANE & al. in prep.).

Upper Cretaceous androecia are three-lobed with two pairs of marginal pollen sacs on the central lobe and a single pair of pollen sacs on the outer margin of the two lateral lobes (Fig. 4 C). Androecia of this kind are known only in *Chloranthus* (Fig. 4 A), and thus plants with some, but not necessarily all of the diagnostic characters of this genus were present at least by the Campanian. The single androecium known from Lower Cretaceous consists of three obovoid stamens that are slightly fused at the base (Fig. 4 D). Each filament is swollen and bears two pairs of pollen sacs. The individual stamens resemble those of *Sarcandra* (Fig. 4 B) and some extant *Winteraceae* (ENDRESS 1986 b, 1987 b), but the staminal aggregation is more like that in *Chloranthus*. The fossil androecium thus exhibits features seen in two chloranthaceous genera, and combines the presumed primitive condition of two pairs of pollen sacs per filament with a more specialized floral arrangement in which the stamens are fused (even if only slightly) into a three-lobed androecium. This fossil provides good evidence of the *Chloranthaceae*, and perhaps the lineage leading to extant *Chloranthus*, before the end of the Early Cretaceous. The swollen filaments, small pollen sacs, small pollen and the apparent presence of pollenkitt are also indicative of insect pollination (FRIIS & al. 1986).

Based on the presence of *Clavatipollenites*-type pollen in well dated sediments (HUGHES & al. 1979, HUGHES & MCDOUGALL 1987) the origin of the *Chloranthaceae* can be inferred to have been as early as the Barremian-Hauterivian. WALKER & WALKER (1984) suggested that the abundance of *Clavatipollenites* and *Asteropollis* in some Mid Cretaceous palynofloras may reflect the first appearance of wind pollination in the angiosperm clade: a conclusion consistent with pollination in extant *Ascarina* and *Hedyosmum*. If this is accepted, then the *Chloranthaceae* were not only widespread in the Cretaceous vegetation of the Northern Hemisphere

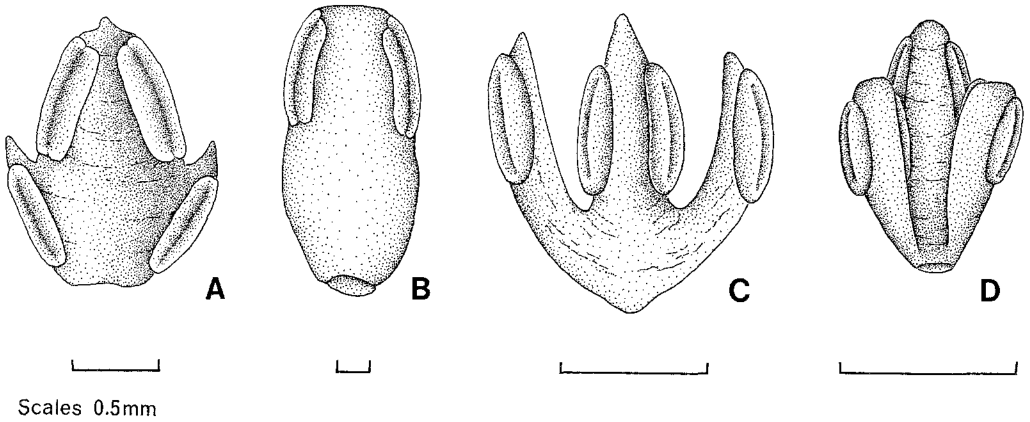

Fig. 4. Androecia of fossil and extant *Chloranthaceae*. *A* Extant *Chloranthus officinalis* BL. (F411034). *B* Extant *Sarcandra chloranthoides* GARDNER (after ENDRESS 1987 b). *C* Fossil androecium Santonian/Campanian, Scania, Sweden (after FRIIS & al., 1986). *D* Fossil androecium, Albian, Maryland, U.S.A. (after FRIIS & al. 1986)

(MULLER 1981), but had also developed both anemophilous and entomophilous pollination syndromes at an early stage in the angiosperm radiation.

Trochodendrales

As most recently circumscribed (ENDRESS 1986a), the *Trochodendrales* comprise four extant genera, *Trochodendron* and *Tetracentron* included in the *Trochodendraceae*, and *Cercidiphyllum* and *Euptelea* included in the monotypic families *Cercidiphyllaceae* and *Eupteleaceae* respectively. Systematically the *Trochodendrales* occupy an analogous position in the *Hamamelidae* to that of the *Chloranthaceae* in the *Magnoliidae*. They exhibit similarities to certain *Magnoliidae* (particularly *Chloranthaceae*), including vesselless wood (*Tetracentron, Trochodendron*), leaves with chloranthoid teeth (*Cercidiphyllum, Tetracentron, Trochodendron*), and "oil cells" (*Tetracentron, Trochodendron*) (ENDRESS 1986a). The wide range in carpel number in the *Trochodendrales* is also similar to the floral plasticity exhibited by the *Magnoliidae* as a whole (ENDRESS 1986a, b). Usually, however, the *Trochodendrales* are placed within the *Hamamelidae* on the basis of their triaperturate pollen grains and other features (ENDRESS 1986a).

The *Trochodendrales* have an extensive fossil record and leaves with the architectural characteristics of this group (actinodromous venation frequently associated with chloranthoid teeth) first appear in the Mid Cretaceous (UPCHURCH & WOLFE 1987). Leaves of "*Populus*" *potomacensis* WARD, *Populophyllum renifome* FONTAINE and *Menispermites potomacensis* BERRY from the Mid-Late Albian of the Potomac Group may be closely related to the *Trochodendrales*, and similar foliage is known from Mid Cretaceous sediments in Eurasia (e.g., KVAČEK 1983), as well as elsewhere in North America (e.g., LESQUEREUX 1892, BELL 1956, BERRY 1921a, SPICER pers. comm.). The reproductive structures of these probable early *Trochodendrales* are unknown, but two later extinct representatives of the group, *Nordenskioldia* and the *Joffrea-Nyssidium* complex, are becoming increasingly well known from studies of Early Tertiary material.

Nordenskioldia. *Nordenskioldia borealis* HEER was first described from the Paleocene of Greenland (then believed to be Miocene) based on infructescences bearing sessile schizocarp-like fruits (HEER 1870). *Nordenskioldia* is now known to be widespread in the latest Cretaceous and Early Tertiary of the Northern Hemisphere (BROWN 1962, KRYSHTOFOVICH 1956, 1958, KRASSILOV 1976, CHANDRASEKHARAM 1974, CRANE & al. 1986a). In North America *Nordenskioldia* persisted into the Miocene (leaves of "*Populus*" *heteromorpha* KNOWLTON and associated in infructescences, Latah flora KNOWLTON 1926, *Carpolithus* spec. Whitebird flora BROWN 1936). The relationships of *Nordenskioldia* remained uncertain until KRYSHTOFOVICH (1956, 1958) recognized the leaves associated with the infructescences and suggested the possibility of a close relationship to *Trochodendron* and *Tetracentron*. Recent studies in the Paleocene of North America (CRANE & al. 1986a, 1988b) support this conclusion, and the discovery of silicified material with well preserved anatomy has clarified many aspects of the structure of this plant.

Infructescences are long, branched (Fig. 9A) and bear numerous sessile fruits (Figs. 5A, B and 7A, B). Each fruit consists of a whorl of about 15 achene-like fruitlets (Figs. 5A and 7D) partially embedded in a shallow cup-like receptacle (Figs. 5A and 7F). Distally the fruit is bilaterally symmetrical (Fig. 5A), but at

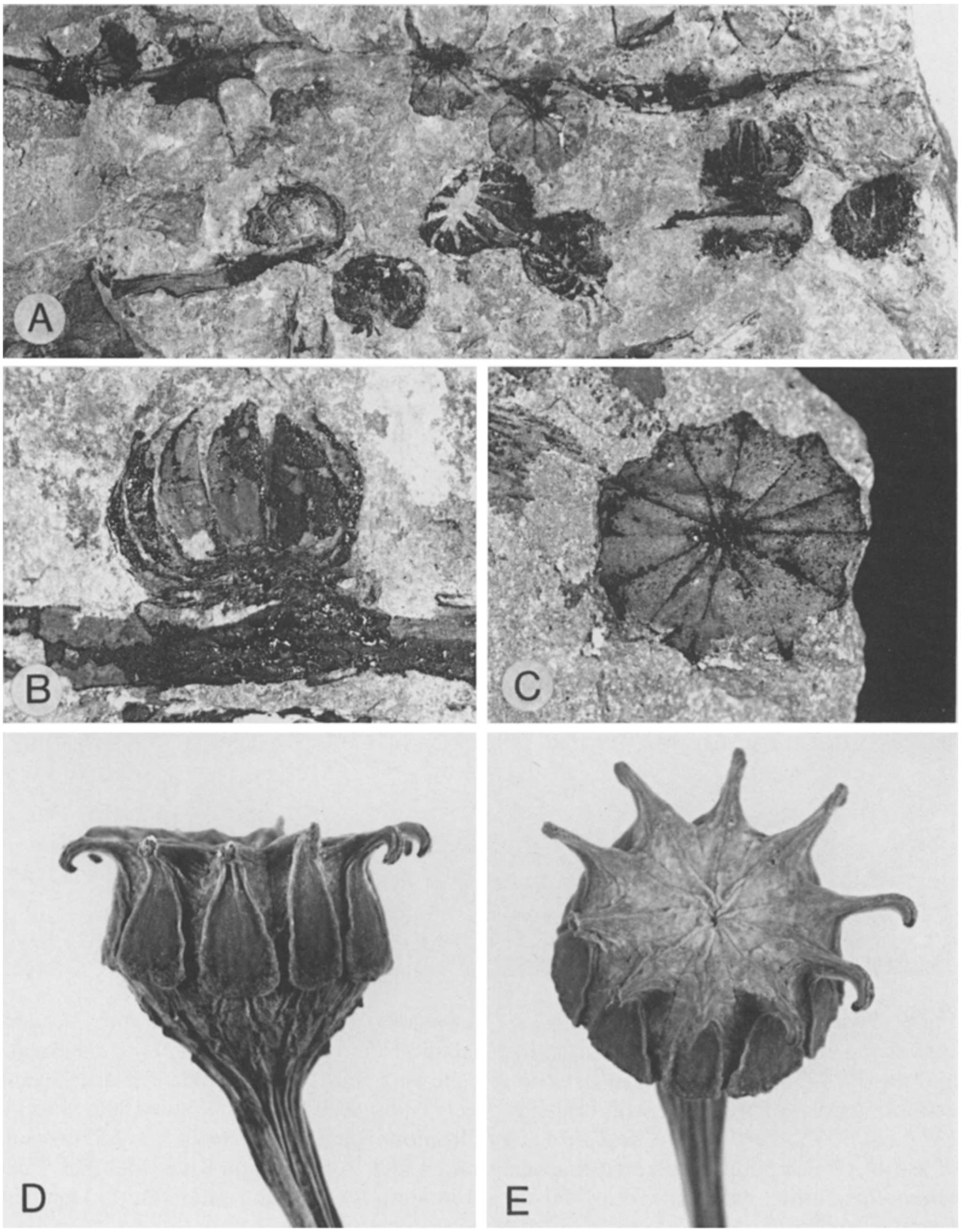

Fig. 5. Fruits of fossil *Nordenskioldia borealis* Heer and extant *Trochodendron aralioides* Sieb. & Zucc. *A* Portion of two *Nordenskioldia* infructescence axes with several attached fruits, note sediment filling between the fruitlets and the persistent collar and central column from which the fruitlets have been shed (PP 34522), × 1.75; *B* lateral view of a fruit showing infructescence axis and separating fruitlets (PP 34527), × 5; *C* basal collar showing positions of attachment of 12 fruitlets (PP 34529), × 5; *D Trochodendron aralioides* Sieb. & Zucc., lateral view of young fruit showing carpels and semi-inferior gynoecium, × 7; *E Trochodendron aralioides* Sieb. & Zucc., oblique apical view of young fruit showing radially arranged carpels and recurved styles, × 7. Fossil material from Tongue River Member, Fort Union Formation, Paleocene (near Melville, Montana)

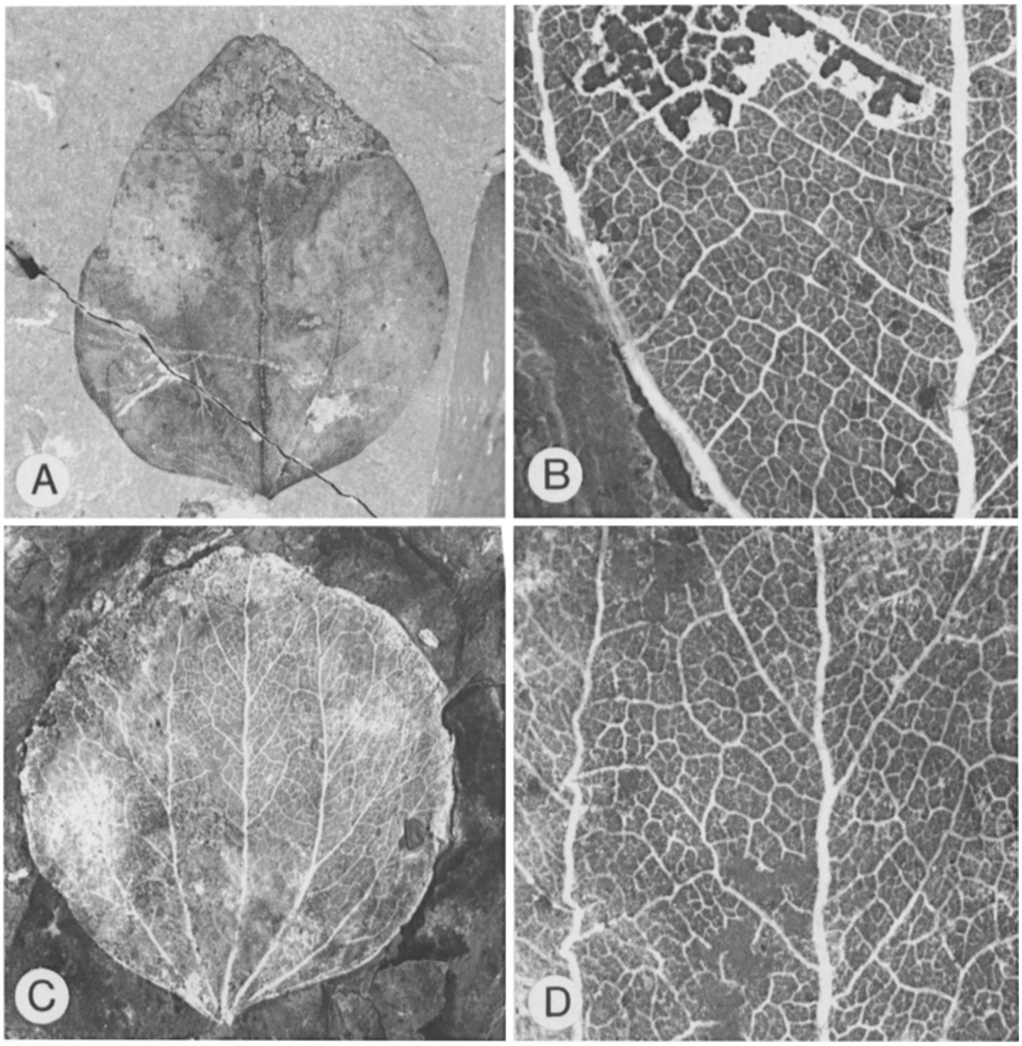

Fig. 6. Fossil leaves ["*Cocculus*" *flabella* (NEWBERRY) WOLFE] associated with *Nordenskioldia borealis* HEER. *A* Small leaf showing actinodromous venation and entire undulate margin (PP 34548), × 3; *B* detail of venation showing third, fourth, and fifth order veins delimiting polygonal areolae with branched freely ending veinlets (cf. WOLFE 1966, HICKEY 1977) (IU 15722-7040), × 6; *C* leaf with actinodromous venation (PP 34538), × 1.5; *D* detail of leaf in *C* with poorly preserved fine venation, × 5; *A* from Tongue River Member, Fort Union Formation, Paleocene (near Melville, Montana); *B* – *D* from Sentinel Butte Member, Fort Union Formation, Paleocene (near Almont, North Dakota)

the attachment to the receptacle the arrangement of the fruitlets is radially symmetrical (Fig. 5 C). Each fruitlet is wedge-shaped in transverse section with two longitudinal bands of fibers along the outer margin (Fig. 7 C, D). Several less prominent bands of fibers form ridges on the radial walls (Fig. 7 C) and laterally compressed specimens show that these ridges occasionally branch and are slightly oblique to the long axis of the fruitlet (Fig. 7 G). The endocarp consists of a mass of obliquely oriented fibers. Each fruitlet contains a single flattened seed with a

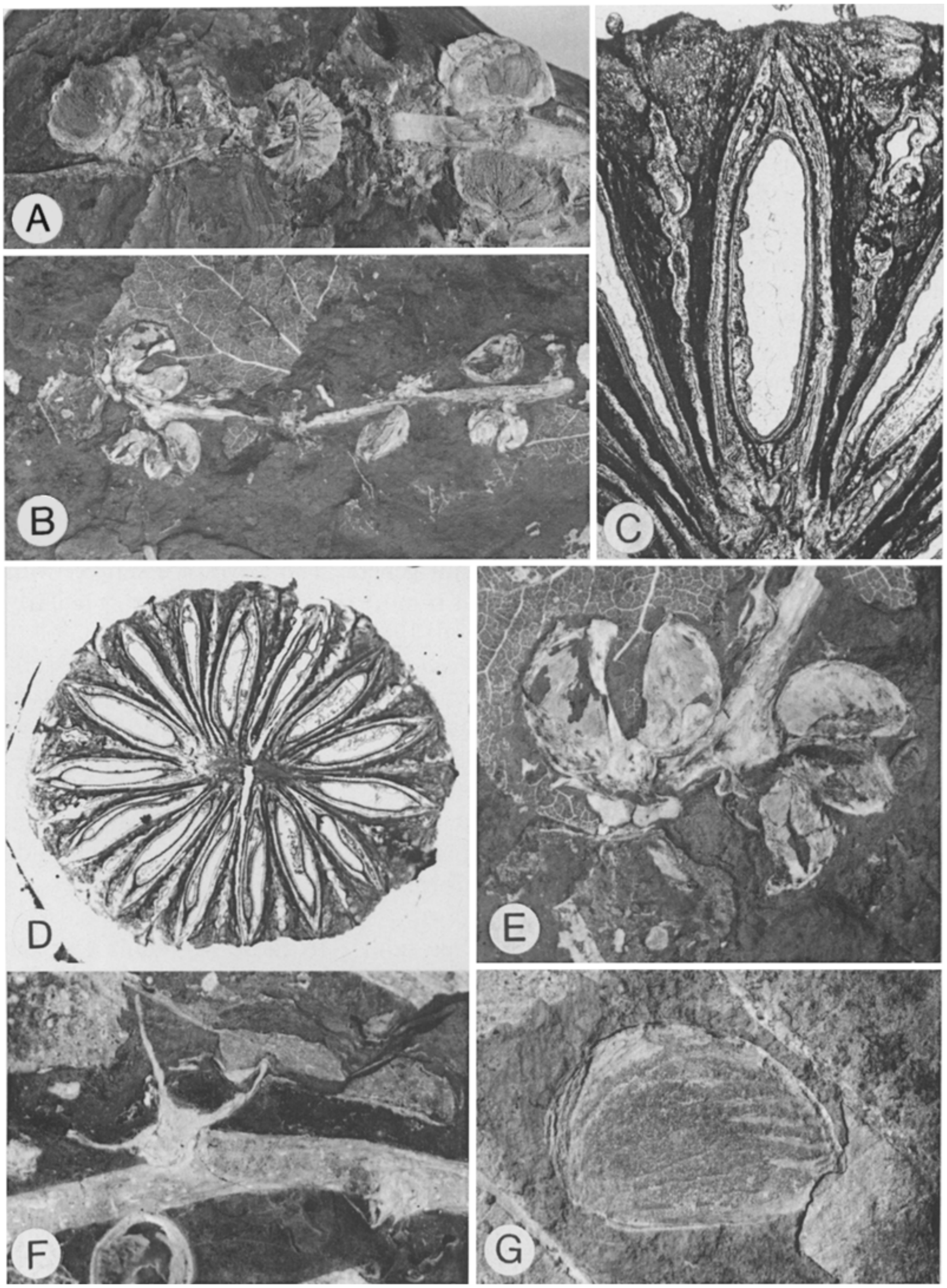

Fig. 7. Infructescences, fruits and fruitlets of *Nordenskioldia borealis* Heer. *A* Portion of infructescence showing four attached fruits (PP 34536), ×2; *B* portion of infructescence axis showing two partially fragmented fruits and associated fruitlets (PP 34537), ×1; *C* transverse section through a silicified fruit in *D* showing a wedge-shaped fruitlet containing a single seed, ×15; *D* transverse section through a silicified fruit showing 15 fruitlets radiating from a central axis (PP 34535), ×5; *E* two partially fragmented fruits from *B* showing separating fruitlets, ×2.5; *E* portion of infructescence axis showing section through persistent collar and central column of a fruit from which the fruitlets have been shed (PP 34425), ×2.5; *G* isolated fruitlet showing vascular strands on the radial walls and attachment scar (PP 34210), ×4. Fossil material from Sentinel Butte Member, Fort Union Formation, Paleocene (near Almont, North Dakota)

narrow flange along each margin (Fig. 7 C). At maturity fruitlets were dispersed individually (Fig. 7 E, G) but the remains of the receptacle persisted on the infructescence axis as a shallow cup often with a central column around which the fruitlets were arranged (Figs. 5 A and 7 E, F). In one specimen this cup shows small elliptical scars that may indicate the position of stamens and hence bisexual flowers. Unfortunately the consistent occurrence of this feature has not yet been established and the stamens, pollen, perianth and sexuality of *Nordenskioldia* flowers are currently unknown.

Shoots of the *Nordenskioldia* plant have been identified by anatomical similarities to infructescence axes (CRANE & al. 1986 a, 1988 b). Both have secondary xylem in which the axial elements consist entirely of tracheids separated by predominantly uniseriate rays. Vegetative axes are clearly differentiated into long and short shoots (CRANE & al. 1988 b). Leaves of the *Nordenskioldia* plant [*"Cocculus" flabella* (NEWBERRY) WOLFE 1966] have been identified by consistent association with the infructescences at numerous localities (KRYSHTOFOVICH 1956, 1958) and have previously been assigned to a variety of extant genera. The leaves are simple, with actinodromous venation and a margin that is more or less entire or has irregularly developed marginal crenations (CRANE & al. 1988 b) (Fig. 6 A, C).

Nordenskioldia is clearly related to *Trochodendron* and *Tetracentron*. The actinodromous leaves and the presence of short shoots are similarities to *Tetracentron* and *Cercidiphyllum*, while the wood anatomy is like that of *Tetracentron* and *Trochodendron*. The syncarpous, semi-inferior gynoecium, the position of the styles and the number of carpels is very similar to that of *Trochodendron* (Fig. 5 D, E). Taken together these features indicate that *Nordenskioldia* is closely related to the *Trochodendraceae*, but more detailed resolution of relationships will require additional morphological and anatomical information.

***Joffrea-Nyssidium* complex.** Fossil leaves similar to those of extant *Cercidiphyllum* are possibly the most abundant element in latest Cretaceous and Early Tertiary floras from middle and high latitudes in the Northern hemisphere (Fig. 8) (BROWN 1939, SCHLOEMER-JÄGER 1958, ILJINSKAJA 1974, CHANDRASEKHARAM 1974, TANAI 1981, CRANE 1984 a). BROWN (1939) first noted the association of these leaves with distinctive elongated infructescences and small winged seeds at numerous localities in North America. Based on the combined information from these three different organs BROWN recognized certain differences from the extant genus but considered the similarities sufficiently strong to assign the fossil remains to *Cercidiphyllum*. Subsequent work has confirmed the association noted by BROWN and has demonstrated winged seeds in permineralized fruits belonging to this complex (*Jenkinsella* REID & CHANDLER 1933, CHANDLER 1961, CRANE 1984 a).

The most fully understood of the Early Tertiary *Cercidiphyllum*-like plants is *Joffrea speirsii* CRANE & STOCKEY known from seedlings, shoots, leaves, pistillate inflorescences, infructescences, seeds, and possibly staminate inflorescences from the Paleocene of southern Alberta, Canada (CRANE & STOCKEY 1985). Similarities to extant *Cercidiphyllum* include opposite phyllotaxy, leaf architecture, distinct long and short shoot differentiation of the vegetative axes, the general organization of the pistillate flowers and inflorescences, the winged seeds with a distinctive "hairpin loop" of the raphe and possibly the organization of the staminate flowers (CRANE & STOCKEY 1985, 1986). Differences from extant *Cercidiphyllum* include

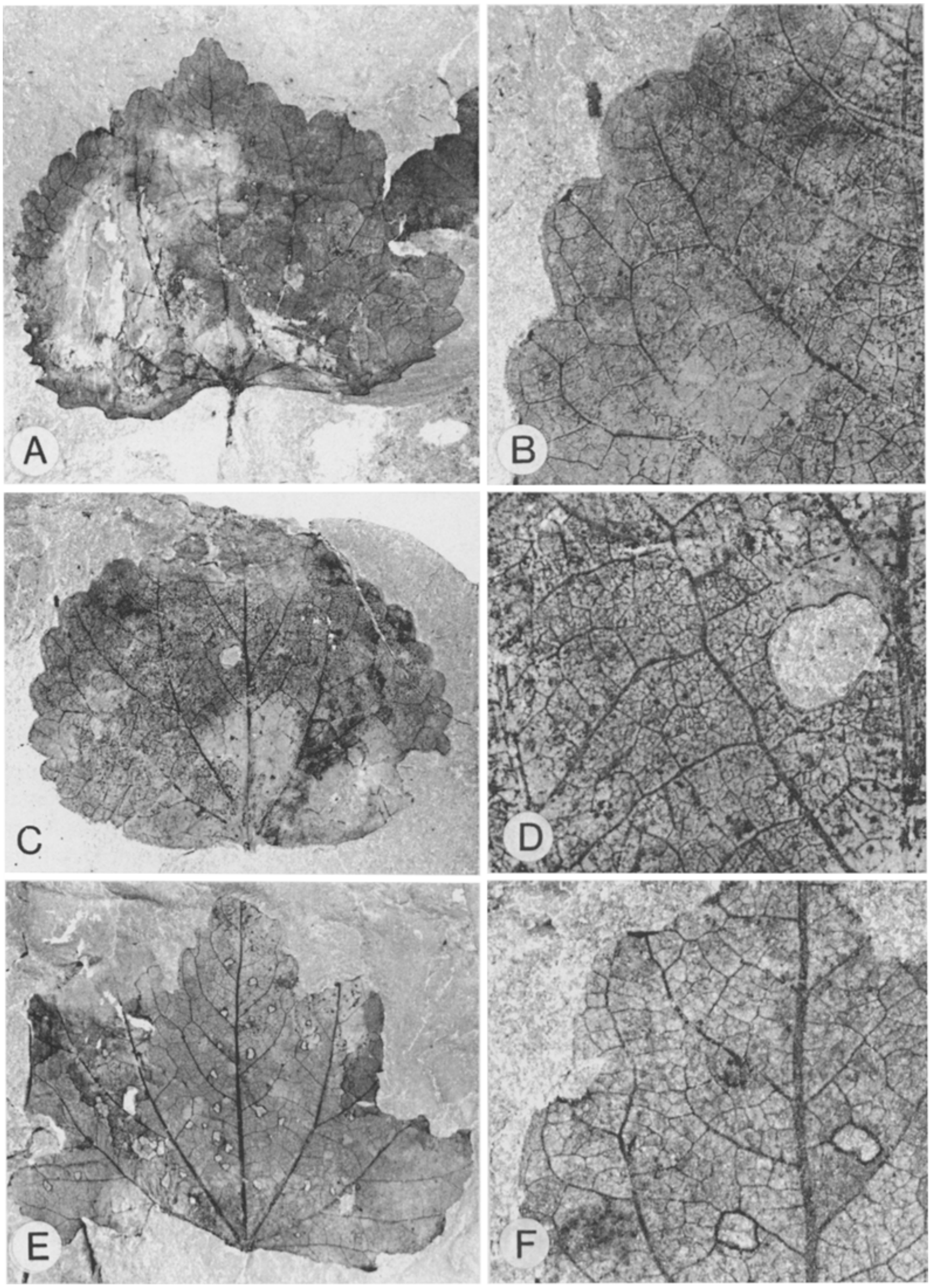

Fig. 8. Leaves of fossil *Cercidiphyllaceae* [*Trochodendroides arctica* (Heer) Brown] – *Nyssidium-Joffrea* complex. *A* Leaf showing actinodromous venation and crenate margin (PP 34516), × 1; *B* margin of leaf in *C* showing glandular (chloranthoid) teeth and details of venation, × 3; *C* leaf showing actinodromous venation, glandular teeth and well preserved fine venation (PP 34519), × 1; *D* detail of fine venation from leaf in *C* showing fourth, fifth and sixth order veins delimiting polygonal areolae with branched freely ending veinlets (cf. Wolfe 1966, Hickey 1977), × 5; *E* lobed leaf with broken margin note similarities in leaf architecture to *A* and *C* (PP 34520), × 1; *F* detail of margin from central lobe of leaf in *E* showing poorly preserved fine venation and glandular teeth, × 5. Fossil material from Tongue River Member, Fort Union Formation, Paleocene (near Melville, Montana)

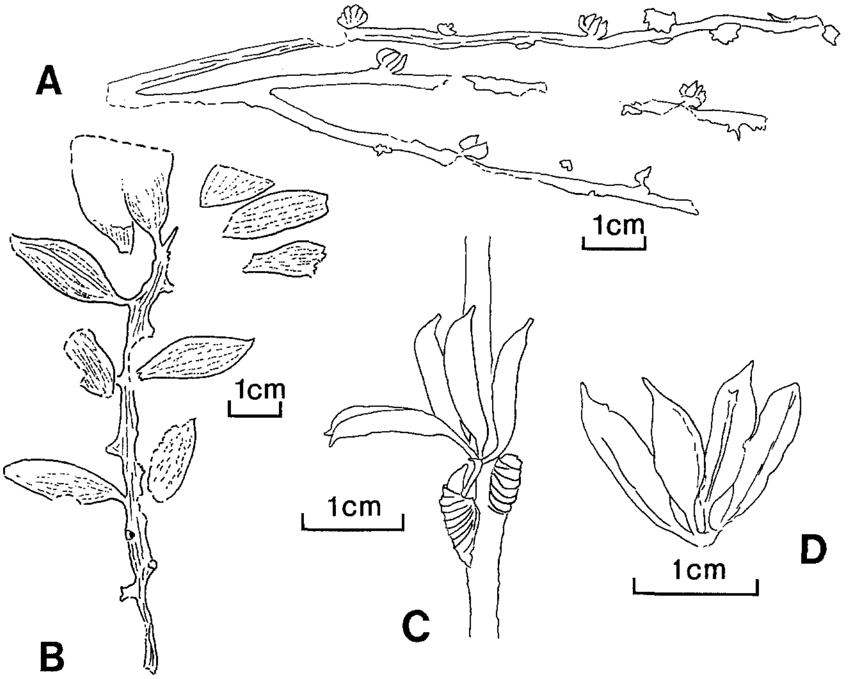

Fig. 9. Infructescences of extant and fossil *Trochodendrales*. *A Nordenskioldia borealis* HEER portion of infructescence with numerous sessile fruits (PP 34546); *B Nyssidium* infructescence (PP 34528); *C* infructescence of extant *Cercidiphyllum japonicum* SIEB. & ZUCC.; *D* fossil infructescence similar to extant *Cercidiphyllum* (UCMP-9309): *A*, *B* from the Tongue River Member, Fort Union Formation, Paleocene (near Melville, Montana); *D* John Day Formation, Oligocene (Pentecost Ranch, John Day Basin, Oregon)

the form of the short shoots, the frequent occurrence of two carpels per flower, the large number of flowers on an elongated inflorescence (Fig. 9 B), details of the anatomy of the follicle wall, the large number of seeds per follicle, anatomy of the seed coat and possibly the large size and number of the bracts in each staminate inflorescence (CRANE & STOCKEY 1985).

Comparisons of *Joffrea* with similar fossil plants from the Early Tertiary of Europe and Asia suggest that there was considerable diversity in phyllotaxy, shoot growth, inflorescence position and the number and crowding of follicles in each infructescence, among extinct *Cercidiphyllaceae* (CRANE & STOCKEY 1986). This diversity is also manifested in the variation that occurs in the fossil foliage of this group and has led to considerable systematic difficulties. Variation in the leaf margin has led to confusion with the foliage of the *Nordenskioldia* complex, and variants with distinctly trilobed laminae (Fig. 8 E, F) have sometimes been referred to "*Ampelopsis*" *acerifolia* (NEWBERRY) BROWN (1962).

Ecologically, the abundance of the *Joffrea-Nyssidium* complex in many fossil floras from fluvial depositional environments, combined with the production of large quantities of small seeds, suggests that these *Cercidiphyllum*-like plants were early colonizers of disturbed habitats during the early Tertiary (CRANE 1987). The occurrence of large numbers of fossil seedlings of both *Joffrea* and extinct *Platanaceae* at the Joffre Bridge locality, Alberta (STOCKEY & CRANE 1983, CRANE &

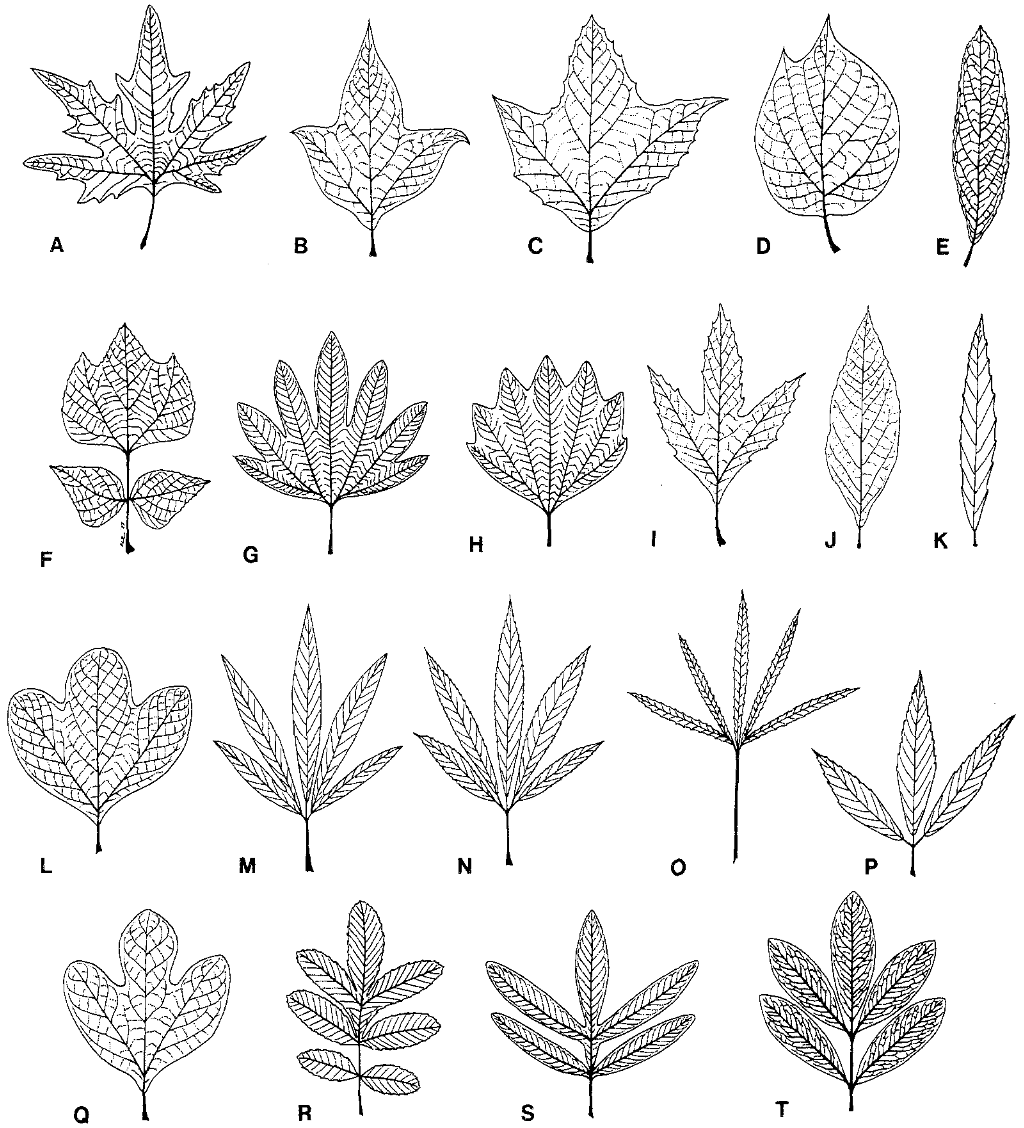

Fig. 10. Foliar variation in extant and fossil *Platanaceae*, and related forms (not to scale). *A Platanus orientalis* L., extant (after Manchester 1986); *B – D Platanus mexicana* Moric., extant (after Nee 1981): *E Platanus kerrii* A Gagnepain, extant (after Manchester 1986); *F Platanites hebridicus* Forbes, Paleocene (after Crane & al. 1988 a); *G Macginitiea angustiloba* (Lesquereux) Manchester, Eocene (after Manchester 1986); *H Macginitiea whitneyi* (Lesquereux) Manchester, Eocene-early Oligocene (after Manchester 1986); *I Platanus schimperi* (Heer) Saporta & Marion, Paleocene (Crane, unpubl.); *J Dicotylophyllum flexuosa* (Newberry) Wolfe (after Crane & al. 1988 b); *K Dryophyllum* spec. Eocene (Crane unpubl.); *L* Generalized *Araliopsoides*, "*Sassafras*" type, Albian (Hickey & Doyle 1977); *M Dewalquea westerhausiana* (Richter) Rüffle, Upper Cretaceous (after Rüffle & Knappe 1977); *N Dewalquea insignis* Hos. & V. D. Marck, Upper Cretaceous (after Rüffle & Knappe 1977); *O Dewalquea pulchella* Knowlton, Cenomanian (after Knowlton 1917); *P Dewalquea fraxinifolia* Johnson & Gilmore, Upper Cretaceous (after Johnson & Gilmore 1921); *Q* Generalized *Araliaephyllum* type, Albian (after Hickey & Doyle 1977); *R Sapindopsis belviderensis* Berry, Albian (after Berry 1921 b); *S Sapindopsis magnifolia* Fontaine, Albian (after Hickey & Doyle 1977); *T Sapindopsis* spec. Albian (after Hickey & Doyle 1977)

Stockey 1985) provides striking evidence that these plants were important Early Tertiary weeds prior to the radiation of many herbaceous groups that today dominate that niche. The *Joffrea-Nyssidium* complex persisted into the Late Eocene (Crane 1984 a) and Oligocene (Becker 1973). Fossil plants with compact inflorescences closely resembling extant *Cercidiphyllum* are first recorded from the Early Oligocene of North America and Europe (Fig. 9 C, D) (Jähnichen & al. 1980).

Platanaceae

The *Platanaceae* comprise a single extant genus divided into two subgenera (Leroy 1982). Subg. *Platanus* includes approximately seven species characterized by the possession of stipules and typical palmate palinactinodromous platanoid leaves (Fig. 10 A – D). The center of distribution for the subgenus is in southwestern North America and Mexico, with one disjunct species (*Platanus occidentalis* L., Fig. 10 A) in eastern North America and another (*P. orientalis* L.) in eastern Europe and western Asia. Subg. *Castaneophyllum* includes only *Platanus kerrii* Gagnepain, a species native to southeastern Asia, that differs from other members of the family in lacking stipules and having elliptical, pinnate veined leaves (Fig. 10 E). The *Platanaceae* have long been known to extend back to the Mid Cretaceous (Lesquereux 1892) but only recently has it become clear that this group may have played an important role in the Mid Cretaceous radiation of dicotyledons (Doyle & Hickey 1976, Hickey & Doyle 1977, Dilcher 1979, Crane & al. 1986 b).

Mid Cretaceous *Platanaceae*. During the Mid Cretaceous the *Platanaceae* are known from leaves, wood, infructescences and both staminate and pistillate flowers (Knappe & Rüffle 1975, Dilcher 1979, Upchurch 1984 a, b, Schwarzwalder & Dilcher 1988, Crane & al. 1986 b, Friis & al. 1988, Manchester pers. comm.). Mid Cretaceous platanoid foliage is characterized by palinactinodromous primary venation but exhibits considerable variation in leaf architecture and cuticular structure (Fig. 10 L, Q) (Schwarzwalder & Dilcher 1987, Upchurch 1984 a). Mid Cretaceous infructescences consists of elongated axes bearing numerous sessile, more or less spherical heads of numerous flowers (Fig. 11 C). Flowers are unisexual with stamens and carpels in fives surrounded by prominent perianth parts (Crane & al. 1986 b). The stamens have short filaments, long pollen sacs and produced very small tricolpate reticulate pollen grains [*Tricolpites minutus* (Brenner) Dettman] approx. 8 – 10 µm in polar length (Crane & al. 1986 b, Friis & al. 1988). The carpels are oblong in shape and differ from those of extant *Platanus* in lacking the mass of hairs that are present at the base of each fruitlet (Fig. 12 D – E).

Platanoid-*Sapindopsis* complex. In addition to palmately lobed platanoid leaves, pinnatifid or pinnate leaves assigned to the fossil genus *Sapindopsis* (Fig. 10 R – T) are a further common component of Mid Cretaceous leaf floras (Berry 1921 b, Doyle & Hickey 1976, Hickey & Doyle 1977), and it has been suggested that foliage of this kind was probably produced by early representatives of the subclass *Rosidae* (Hickey & Wolfe 1975, Doyle & Hickey 1977). *Sapindopsis* foliage exhibits considerable variation in gross morphology, venation and the form of the margin (Berry 1921 b, Hickey & Doyle 1977) and many specimens exhibit interesting similarities to the leaves of Mid Cretaceous platanoids. Some forms have trilobed terminal leaflets with palinactinodromous primary venation closely resembling that in contemporaneous platanoid leaves (Fig. 10 R) (HICKEY & DOYLE 1977). Other variants exhibit details of tooth venation resembling that seen in some platanoid foliage. This partial intergradation in the morphology of platanoid and *Sapindopsis* leaves is paralleled by similarities in cuticular structure (UPCHURCH 1984 a) and has been used to suggest a close phylogenetic relationship between these two groups of Mid Cretaceous angiosperms. By extension a close, possibly sister group, relationship has been inferred between the *Hamamelidae* and *Rosidae* (HICKEY & WOLFE 1975, DOYLE & HICKEY 1976, HICKEY & DOYLE 1977).

The reproductive structures of *Sapindopsis* plants are unknown but at some Mid Cretaceous localities where platanoid leaves are either absent or rare, *Sapindopsis* foliage is associated with inflorescences of the platanoid type. These observations have led to the suggestion that in reproductive structure, as well as leaves, the platanoid and *Sapindopsis* groups may have exhibited significant similarities (HICKEY & DOYLE 1977). Recent work in the Potomac Group of eastern North America has provided some support for this conclusion (CRANE & al. 1986 b). At the West Brothers locality *Sapindopsis* foliage dominates the leaf flora, and in addition to platanoid inflorescences sieving of unconsolidated sediments has yielded other more or less spherical inflorescences that are sessile along the inflorescence axis (CRANE & al. 1986 b). Each spherical head consists of numerous small flowers in which the central floral organs are arranged in fives. It remains to be determined whether these organs are stamens or carpels but as in the platanoid flowers they are surrounded by prominent perianth parts. These reproductive structures differ from the platanoid inflorescences that occur at the same locality in their size, the smaller number of flowers per inflorescence, and the presence of clumps of pollen grains with distinct endoapertures (CRANE & al. 1986 b). Cuticles isolated from these inflorescences more closely resemble those from *Sapindopsis* foliage rather than the cuticles isolated from the rare platanoid leaves at this locality (UPCHURCH pers. comm.). Although these results are preliminary the data presently available indicate that the reproductive structures of at least some Mid Cretaceous platanoid and *Sapindopsis* plants were similar.

Late Cretaceous and early Tertiary *Platanaceae*. Following their first appearance in Mid Cretaceous sediments the *Platanaceae* persist as an important component of the angiosperm fossil record throughout the Late Cretaceous and Early Tertiary. Few of these plants are well understood although detailed information is now available on several *Platanaceae* from the Upper Cretaceous (Santonian-Campanian) of southern Sweden and North Carolina (FRIIS 1985, FRIIS & al. 1988), and the Early Tertiary of Europe (CRANE & al. 1988 a) and western North America (MANCHESTER 1986).

Staminate inflorescences from the Santonian-Campanian of Europe and North America conform to the structure of Mid Cretaceous flowers in having well developed perianth parts and five stamens with short filaments and long pollen sacs in each flowers (FRIIS 1985). Flowers from southern Sweden have especially prominent perianth parts and stamens in which the connective is expanded distally to form a pronounced conical extension above the pollen sacs (FRIIS 1985, FRIIS & al. 1988). Dispersed platanoid stamens from the same locality are more like those of the extant genus in having a peltate distal expansion of the connective (FRIIS 1985). Flowers from North Carolina have a similar peltate connective and also

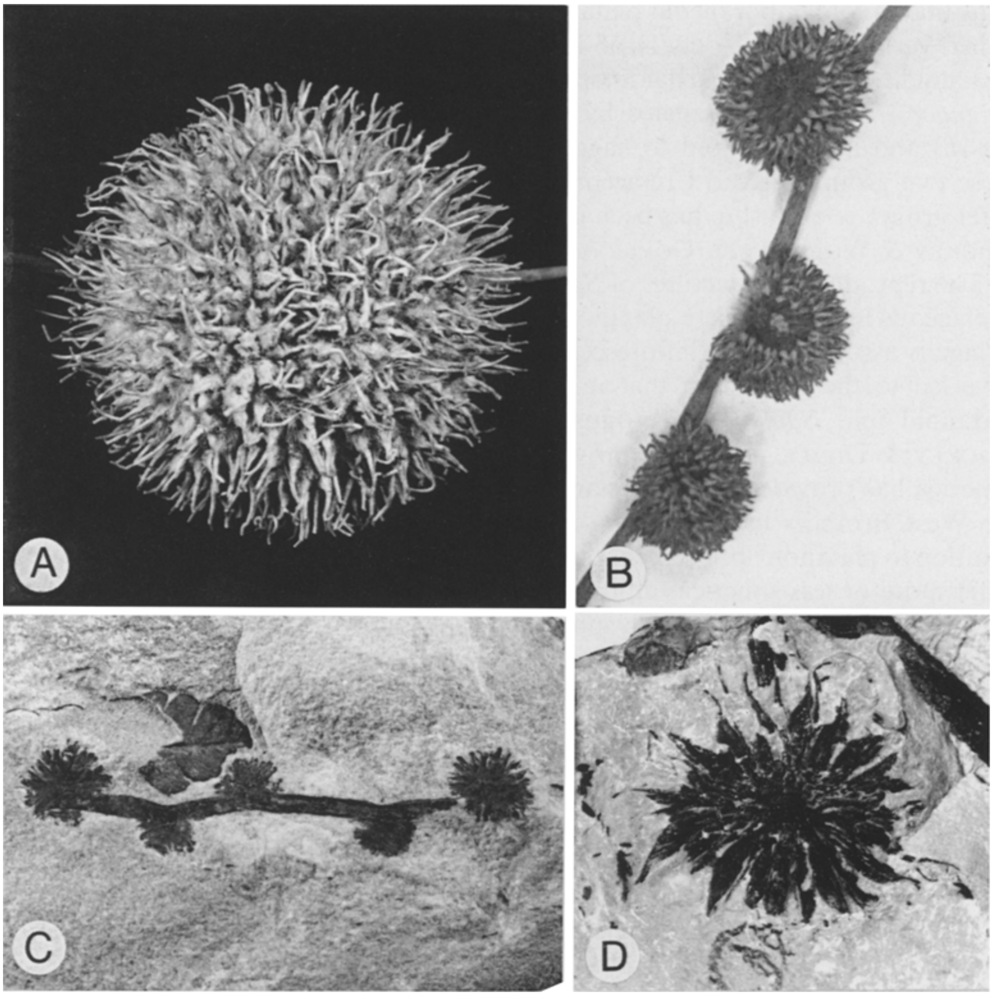

Fig. 11. Extant and fossil platanoid infructescences. *A Platanus orientalis* L., × 2; *B Platanus kerrii* Gagnepain (BM, Kerr, April 28, 1932), × 2; *C "Sparganium" aspensis* Brown, Aspen Shale (see Brown 1933, late Albian-Cenomanian) Wyoming (USNM 41147), × 2; *D Macginicarpa*-like infructescence, Wind River Formation (Middle Eocene), Wyoming (PP 10151), × 2

differ from the Swedish material in having less prominent perianth parts. In all of this Late Cretaceous staminate material the pollen grains are smaller than those of the extant genus. Pistillate reproductive structures associated with the staminate material are less well preserved, but the limited information available suggests that the fruitlets were also derived from carpels with five flowers and lacked the mass of basal hairs seen in the extant genus (Friis & al. 1988).

The most completely understood of Early Tertiary *Platanaceae* is the "*Macginitiea angustiloba* plant" known from the middle to late Eocene of North America on the basis of leaves (Fig. 10 G), petiole and stem anatomy, pistillate inflorescences, fruits, staminate inflorescences and pollen (Manchester 1986). In several respects, this plant is more similar to the Late Cretaceous *Platanaceae* than the extant genus.

Flowers are unisexual with well developed perianth parts and carpels or stamens in fives. The fruitlets show no indication of the prominent hairs that occur on those of the extant genus (Fig. 12). The pollen is also smaller (12 – 16 µm) than that of extant *Platanus*. As in the staminate flowers from Sweden the stamens have distally elongated connectives but are unusual in that the connectives of the five stamens in an individual flower are held together by a mass of hairs. The androecium from individual flowers adheres together even after it is shed from the inflorescence (Manchester 1986).

Leaves of *Platanites hebridicus* Forbes from the Paleocene of northwest Scotland provide interesting information on the foliar variability among Early Tertiary elements of the platanaceous clade (Crane & al. 1988 a). Each leaf is pinnate and consists of a shallowly three-lobed terminal leaflet and two smaller asymmetric lateral leaflets (Fig. 10 F). In all architectural features the terminal leaflet closely resembles the leaves of extant *Platanus* subg. *Platanus*, but the presence of distinct lateral leaflets is unknown in this group. Staminate reproductive structures associated with *Platanites hebridicus* resemble those of extant *Platanus* in having stamens with a peltate distal expansion of the connective, and pollen grains within the size range of those of the extant species (16 – 22 µm). The number of stamens per flower is unknown. Pistillate reproductive structures associated with *P. hebridicus* are

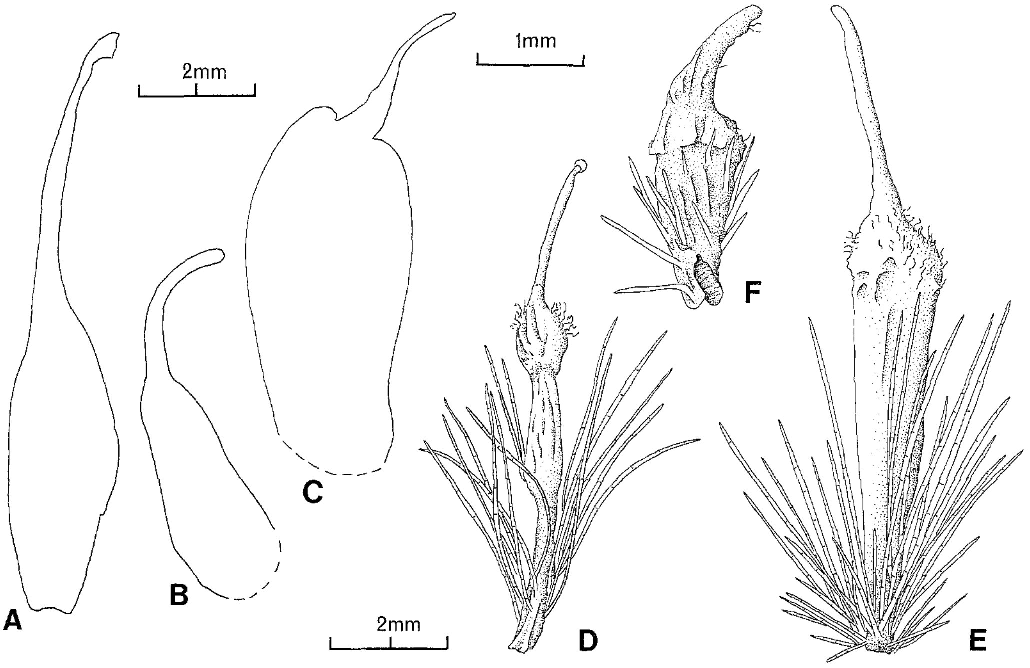

Fig. 12. Fruitlets of extant and fossil *Platanaceae*. *A* Fruitlet associated with *Platanus schimperi* (Heer) Saporta & Marion (PP 34558), from Woolwich & Reading Formation, Paleocene (Cold Ash Quarry, Berkshire, England); *B* fruitlet associated with *Platanites hebridicus* Forbes (v. 25058), from Interbasaltic Leaf Beds, Paleocene (Mull, Scotland); *C* Fruitlet of *Macginicarpa glabra* Manchester (IU 5146), from Clarno Formation, Middle Eocene (West Branch Creek, Oregon) (after Manchester 1986); *D Platanus orientalis* L.; *E Platanus mexicana* Moric.; *F Platanus kerrii* Gagnepain (BM, Kerr, April 28, 1932). All fruitlets except *F* to same scale (2 mm)

poorly understood but the number of achenes per fruiting head and achene shape resembles that in other Early Tertiary *Platanaceae* such as *Macginitiea* (Figs. 11 D and 12 B, C). The number of achenes per flower is unknown.

Macginitiea and *Platanites* both document the considerable foliar variation in the platanoid clade during the early Tertiary. Additional material from the Paleocene of North America indicates that other compound leaves previously assigned to *Cissus marginata* (LESQUEREUX) BROWN (1962), and *Negundo fremontensis* BERRY (1931) may also be platanaceous. In addition certain simple Paleocene leaves [Fig. 10 J, *Dicotylophyllum flexuosum* (NEWBERRY) WOLFE] previously assigned to *Quercus* (BROWN 1962) and *Meliosma* (HICKEY 1977) may also be referable to the family. The foliar variability of the *Platanaceae* during the Early Tertiary thus appears to have encompassed morphologies ranging from simple to palmate to pinnate (Fig. 10 F – J)

Chronological trends in the platanoid lineage. Although our current understanding of the fossil record of the *Platanaceae* is too poor for detailed cladistic analysis several chronological trends in floral structure seem to be clear. Primitive platanoid flowers were unisexual, delimited by a distinct perianth, and each contained five carpels or stamens. This basic plan seems to have persisted at least until the Eocene although throughout the Upper Cretaceous and Early Tertiary there was evidently considerable variability in other characters including the development of the perianth, the structure of stamens and leaf morphology.

In general, throughout the history of this clade there seems to be a trend toward increasing pollen size but while it is likely that the Mid Cretaceous representatives were insect-pollinated this is less certain for some Early Tertiary fossils (e.g., *Platanites*). Within the platanoid clade there has apparently been a trend toward wind-pollination although curiously the staminodes present in some pistillate flowers of the extant genus (CRONQUIST 1981) have not been detected in fossil material. The trend to anemophily was apparently accompanied by reduction in the size of the perianth parts. Extant *Platanus* seems to represent the culmination of this trend in which the perianth is so reduced that it no longer constrains the arrangement of carpels and stamens during floral development (see ENDRESS 1987 a), thus accounting for the highly variable number of achenes in extant platanaceous infructescences. Possibly associated with this process was a decrease in the number of heads per infructescence, an increase in the size of each fruiting head (Fig. 11), an increase in the number of achenes per fruiting head (Fig. 11) and a concomitant change in the shape of platanaceous achenes from the ellipsoidal forms of the Early Tertiary to the obovoid forms of the extant genus (Figs. 11 and 12). Possibly the characteristic dispersal hairs associated with the achenes of extant *Platanus* (Fig. 12 D – F) also became well developed at this time.

In the fossil record it is difficult to assess the time of first appearance of this suite of characters associated with extant *Platanus,* but fruiting heads with densely crowded obovoid achenes that unequivocally have a distinct tuft of hairs at the base are first recognized in the latest Eocene or earliest Oligocene of the John Day Basin in eastern Oregon (MANCHESTER pers. comm.). Whether these fossils exhibit the floral characteristics of the extant genus is currently unknown.

Platanoid-*Debeya-Dewalquea* complex. Palmately compound leaves with a distinctive pedate arrangement of leaflets are common in Late Cretaceous and Early

Tertiary floras from the Northern hemisphere and have been assigned to the genera *Debeya* and *Dewalquea* (Fig. 10 M – P) (SAPORTA & MARION 1873, KNOWLTON 1917, STOCKMANS 1932, KRASSILOV 1973, NĚMEJC & KVAČEK 1975). *Debeya-Dewalquea* foliage has been compared to leaves of extant *Araliaceae, Sterculiaceae*, and certain *Ranunculaceae* (*Helleborus*) but their systematic position has generally been considered uncertain (SAPORTA & MARION 1873, KNOWLTON 1917). JOHNSON & GILMORE (1921) compared *Dewalquea* to leaves of extant *Juglandaceae* but more recently it has been recognized that *Debeya-Dewalquea* leaves exhibit similarities in morphology, venation and cuticular structure to extant and fossil *Fagaceae* and *Platanaceae*. Some taxa (*Debeya pentaphylla* VELENOVSKÝ, *Debeya coricea* (VELEN.) KNOBL., KVAČEK 1983) are particularly similar to the "*Aralia*" and "*Platanus*" components of the Mid Cretaceous platanoid complex (NĚMEJC & KVAČEK 1975, KVAČEK 1983) while others [*Debeya insignis* (HOS. & MARCK.) KNOBL., *Dewalquea hibernica* JOHNSON & GILMORE 1921, NĚMEJC & KVAČEK 1975, KVAČEK 1983] have been compared with leaves of extant *Castanopsis* (*Fagaceae*, RÜFFLE 1978) or the simple leaved *Platanaceae. Dicotylophyllum flexosum* (NEWBERRY) WOLFE (Paleocene, CRANE & al. 1988 b) *Platanus kerrii* GAGNEPAIN (extant), and *P. neptuni* BŮŽEK, HOLÝ & KVAČEK (1967, Miocene). *Dewalquea fraxinifolia* JOHNSON & GILMORE (1921) has been reassigned to *Platanus* largely on the basis of cuticular similarities (WALTHER 1985).

Leaves of *Dewalquea pulchella* KNOWLTON (1917) (Fig. 10 O) are abundant in the Frontier Formation (Cenomanian-Turonian, NICHOLS & JACOBSON 1982) near Cumberland Gap in southwestern Wyoming. The leaves are five-lobed and exhibit considerable variation in the extent to which the lamina is divided (KNOWLTON 1917, CRANE unpubl. results). In many specimens the lamina of the central lobe is free from that of the lateral lobes and may have a well developed petiolule (cf. Fig. 10 N, P). Isolated leaflets of this material closely resemble leaves of *Dryophyllum* (Fig. 10 K) and leaflets of other *Dewalquea* species have occasionally been assigned to this genus (RÜFFLE 1978). *Dryophyllum* is known to be related to extant *Fagaceae* based on studies of leaf venation and cuticles in Early Tertiary material (DILCHER 1971, RÜFFLE & al. 1976, JONES 1986).

The *Debeya-Dewalquea* complex has therefore been regarded as "intermediate" between Mid Cretaceous platanoids and Late Cretaceous-Early Tertiary *Fagaceae* (RÜFFLE & KNAPPE 1977, RÜFFLE 1980, JONES 1986). In certain features of venation, details of marginal teeth and cuticular structure these leaves overlap with the foliar variability seen in the platanoid-*Sapindopsis* complex (Figs. 10 and 13). Information on the reproductive structures of these plants will be necessary to clarify further their phylogenetic position.

Discussion and conclusions

The paleobotanical record indicates that the lineages leading to extant *Chloranthaceae, Platanaceae* and *Trochodendrales* were already differentiated in the Mid Cretaceous, and that the Aptian-Cenomanian interval was the critical phase during which nonmagnoliid dicotyledons underwent their initial major radiation. Although the *Magnoliidae* were also present and diversifying at this time (*Lactoridaceae*, ZAVADA & TAYLOR 1987, *Magnoliaceae*, DILCHER & CRANE 1984, ?*Myristicaceae*, WALKER & WALKER 1984, *Winteraceae*, WALKER & al. 1983, *Magnoliidae* incertae

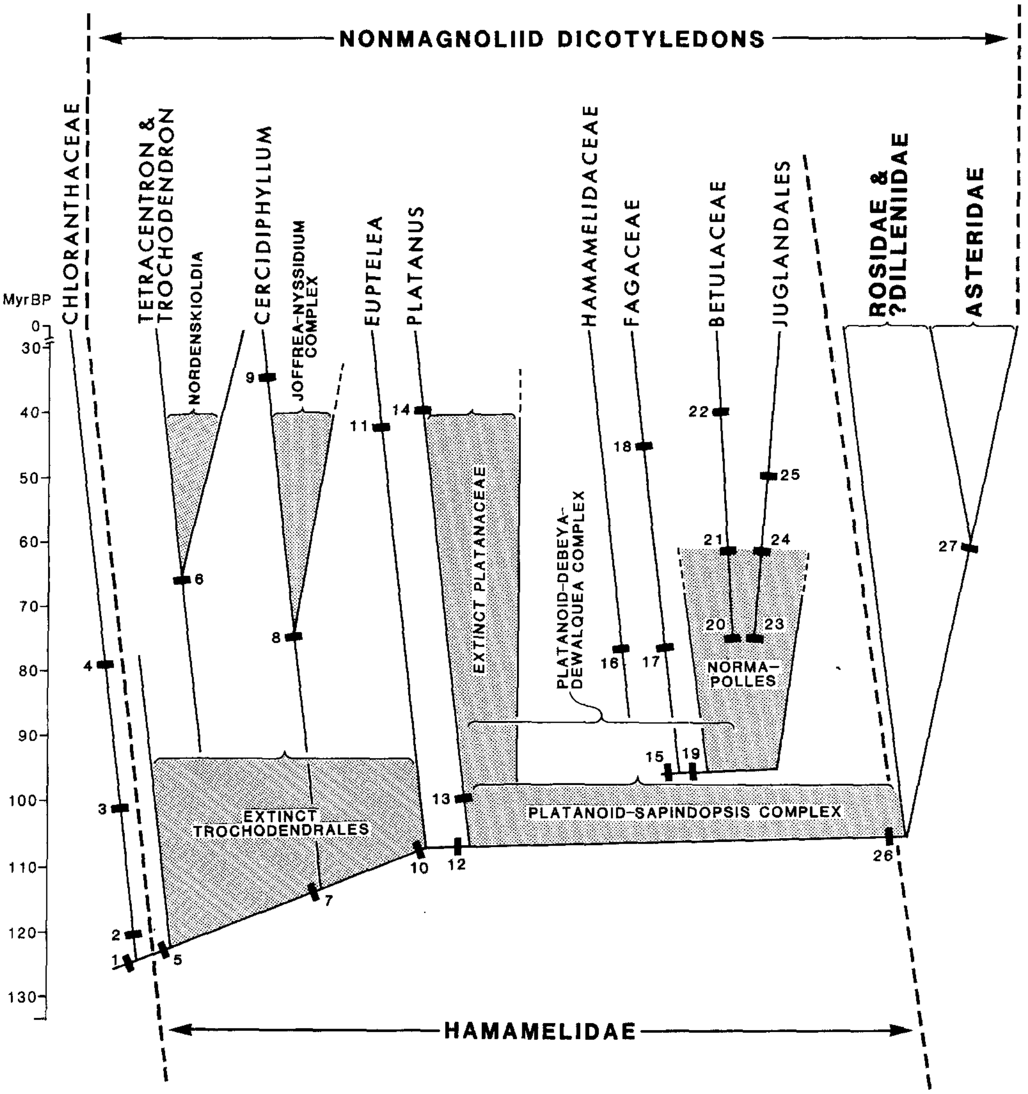

Fig. 13. Diagram summarizing hypothesized relationships between selected dicotyledons showing approximate times of appearance in the fossil record and possible position of critical fossil taxa. The *Caryophyllidae* and *Ranunculidae* are omitted. Numbers refer to possible autapomorphies and synapomorphies and are summarized below (see also text). Cited literature is the source for systematic and stratigraphic data. Specific reference to time of appearance in the fossil record is only made if this conflicts with the position on the diagram dictated by patterns of relationships. 1 Valvate anther dehiscence, lost in *Cercidiphyllum* and nodes 15 and 26, rudimentary in *Euptelea* (Endress 1986a, 1987b); not known in the fossil record until Mid Albian (Friis & al. 1986): chloranthoid teeth, modified at node 10 (Hickey & Wolfe 1975, Endress 1986a); not known in fossil record until the Aptian (Upchurch 1984b): reduction of tepals, ? replaced by "staminodal petals" at node 12 (Walker & Walker 1984, Endress 1986a); earliest occurrence in fossil record uncertain. 2 *Clavatipollenites hughesii* (Hughes & al. 1979) indicating possible presence of *Ascarina-Hedyosmum* type *Chloranthaceae* (Walker & Walker 1984), similar grains may extend into the Hauterivian (Hughes & McDougall 1987). 3 Trilobed androecium as in *Chloranthus* but each stamen with two pairs of pollen sacs as in *Sarcandra* (Friis & al. 1986, Crane & al. in prep.). 4 Trilobed androecium with one pair of pollen sacs on each

sedis, e.g., *Lesqueria*, "?*Williamsonia*" *recentior*, CRANE & DILCHER 1984, *Caloda*, DILCHER & KOVACH 1986, *Prisca* RETALLACK & DILCHER 1981) the radiation of "higher" dicotyledons may have been a major factor in the marked reduction in diversity, and eventual elimination of several groups of fossil gymnosperms. In association with this radiation, several features including triaperturate pollen grains, vessels, palmate and pinnate foliage, and pentamerous floral organization appear in the fossil record for the first time. In addition, the stabilization of whorled, pentamerous floral anthotaxy may have been a significant factor in facilitating further modification of floral structure and the elaboration of associated pollination mechanisms. Although these features were evidently acquired independently in several angiosperm lineages (BAILEY 1944, KUBITZKI 1987), it was at the level of

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lateral lobe as in *Chloranthus* (FRIIS & al. 1986, CRANE & al. in prep.). 5 Triaperturate pollen (DOYLE 1978) not known in fossil record until Barremian-Aptian boundary: actinodromous leaf venation; not known in fossil record until Albian (HICKEY & DOYLE 1977). 6 *Nordenskioldia, Tetracentron, Trochodendron* clade defined by presence of a sessile syncarpous semi-inferior gynoecium (ENDRESS 1986 a, CRANE & al. 1986 a, 1988 b). 7 Loss of "tepalar" petals (see WALKER & WALKER 1984, ENDRESS 1986 a); earliest occurrence in fossil record uncertain: vessels (BAILEY 1944, STOPES 1912, HUGHES 1976). 8 Inflorescences diagnostic of *Cercidiphyllaceae* including the *Joffrea-Nyssidium* complex (ENDRESS 1986 a, DORF 1942, CRANE 1984 a, CRANE & STOCKEY 1985). 9 Inflorescences diagnostic of extant *Cercidiphyllum* (JÄHNICHEN & al. 1980, MANCHESTER pers. comm.). 10 Reduction of lateral veins of chloranthoid teeth (HICKEY & WOLFE 1975). 11 Pollen diagnostic of extant *Euptelea* (MULLER 1981). 12 Flowers with five stamens and/or carpels (CRANE & al. 1986 b, FRIIS & al. 1988, KUBITZKI 1987), modified at node 15, extant *Platanus* (see text) and many *Rosidae:* origin of "staminodal petals" (see WALKER & WALKER 1984). 13 Unisexual platanoid flowers (CRANE & al. 1986 b, FRIIS & al. 1988). 14 Obovoid achenes with basal hairs diagnostic of extant *Platanus* (MANCHESTER, pers. comm.). 15 Modification of apocarpous pentamerous gynoecium to syncarpous tricarpellate ovary (KUBITZKI 1987, FRIIS & CREPET 1987). 16 Flowers of *Hamamelidoideae* with a pair of anther thecae opening by a single valve (FRIIS 1985), diagnostic of extant *Dicoryphe, Ostrearia, Neostrearia, Noahdendron, Trichocladus,* and *Hamamelis* (also *Exbucklandia, Symingtonioideae* ENDRESS 1989). 17 Bisexual flowers of probable *Fagales* (TIFFNEY & FRIIS in TIFFNEY 1986). 18 Cupulate fruits ? diagnostic of extant *Quercus* or *Lithocarpus* (BONES 1979) and ? *Castanea* (CREPET & DAGHLIAN 1980); infructescences and inflorescences of trigonobalanoid and *Castanopsis/Chrysolepis* type first appear slightly earlier around the Paleocene/Eocene boundary (CREPET & NIXON 1986). 19 Triporate pollen (DOYLE 1978). 20 Pollen with arci diagnostic of extant *Alnus* (*Betulea*) (MIKI 1977, MULLER 1981). 21 Fruits diagnostic of extant *Corylus* (*Coryleae*), *Palaeocarpinus* also present (CRANE 1981, 1984 b). 22 Fruits diagnostic of extant *Carpinus, Ostrya* and extinct *Asterocarpinus* (*Coryleae,* CRANE 1984, MANCHESTER & CRANE 1987). 23 Bisexual flowers with in situ Normapolles pollen diagnostic of extant *Juglandales* (FRIIS 1983). 24 Fruits diagnostic of extant *Cyclocarya* (MANCHESTER & DILCHER 1982, CRANE & al. 1988 b, MANCHESTER 1987). 25 Infructescences, fruits, inflorescences, pollen and leaves diagnostic of extant *Platycarya* (REID & CHANDLER 1933, WING & HICKEY 1984, MANCHESTER 1987). 26 Pinnatifid and pinnately compound leaves (HICKEY & WOLFE 1975, DOYLE & HICKEY 1976, HICKEY & DOYLE 1977). 27 Sympetalous flowers "in which the stamens are isomerous and alternate with the corolla-lobes, or fewer than the corolla lobes" (CRONQUIST 1981: 852): earliest occurrence in fossil record uncertain: pollen diagnostic of *Apocynaceae* and *Gentianaceae* (MULLER 1984) the *Hamamelidae* that they apparently became fixed as part of the "Bauplan" of the majority of living dicotyledons.

Although the *Chloranthaceae, Trochodendrales* and *Platanaceae* may have been involved in the transition from the magnoliid grade to "higher" dicotyledons the details of how these taxa are related remain uncertain. One hypothesis of relationships among these groups is given in Fig. 13, based largely on the views of others (HICKEY & WOLFE 1975, DOYLE & HICKEY 1976, ENDRESS 1977, CRONQUIST 1981, WALKER & WALKER 1984) as well as the recently obtained neobotanical and paleobotanical information reviewed here. The suggestions embodied in this hypothesis need to be tested by a more comprehensive analysis of extant taxa, but it is also clear that the considerable extinct diversity in the *Hamamelidae* will require a more refined understanding of fossil taxa for detailed resolution of phylogenetic relationships (see CRANE 1985, DOYLE & DONOGHUE 1987). Important paleobotanical priorities will be: recognition of the pistillate reproductive structures of Mid Cretaceous *Chloranthaceae*, additional information on early *Trochodendrales*, and clarification of reproductive structures in the *Sapindopsis* and *Debeya-Dewalquea* groups. Much of this work requires emphasis on the Mid Cretaceous fossil record, but experience with extinct *Platanaceae* (*Macginitiea*), *Trochodendrales* (*Joffrea-Nyssidium, Nordenskioldia*) and *Fagaceae* (*Fagopsis*, MANCHESTER & CRANE 1983) suggests that useful information can also be obtained from Early Tertiary material. With respect to the "higher *Hamamelidae*" (e.g., *Betulaceae, Juglandaceae, Myricaceae*) the major outstanding question concerns the position of plants that produced the abundant and diverse triporate *Normapolles* pollen in eastern North America and Europe during the Late Cretaceous. While it is now clear that at least some *Normapolles* taxa were closely related to the extant *Juglandales* (FRIIS 1983, 1984, 1985), their position with respect to the *Fagales* and other *Hamamelidae* remains unresolved and will be critical to further clarification of relationships among extant *Hamamelidae*.

Note added in proof. The demonstration of vessels in the root secondary xylem of *Sarcandra glabra* (THUNB.) NAKAI (CARLQUIST, S., 1987: Presence of vessels in wood of *Sarcandra* (*Chloranthaceae*): comments on vessel origins in angiosperms. – Amer. J. Bot. **74**: 1765 – 1771) is consistent with the pattern of relationships among extant *Chloranthaceae* summarized in Fig. 3 B. If vessels are general within the genus then there is no necessity to invoke either loss of vessels in *Sarcandra*, or parallel acquisition of vessels in *Chloranthus* and the *Ascarina-Hedyosmum* clade.

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Address of the author: PETER R. CRANE, Department of Geology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605, U.S.A.