FRUIT AND SEED DISPERSAL AND THE EVOLUTION OF THE HAMAMELIDAE[1]

BRUCE H. TIFFNEY[2]

ABSTRACT

The assumptions (1) that the Hamamelidae attained their zenith in the Cretaceous and, (2) that abiotic dispersal dominated in Cretaceous angiosperms, suggest that dispersal mode could be used as a character in evaluating families questionably associated with the Hamamelidae. A review of modern dispersal characters indicates that most "lower" Hamamelids are abiotically dispersed, but that several putatively derived families (e.g., Fagaceae, Moraceae) predominantly possess biotic dispersal. In many cases the dispersal mechanisms of a family are the same in the fossil record and the present day. However, in the Juglandaceae and Fagaceae the fossil record indicates a switch in dominance from abiotic to biotic dispersal around the Cretaceous-Tertiary border. Circumstantial fossil and modern evidence suggests a similar transition in the Moraceae/Cecropiaceae/Urticaceae and possibly the Ulmaceae. Thus, modern dispersal mode may not reflect the primitive dispersal mode in a lineage. Fossil dispersal evidence supports assignment of the Juglandaceae and Fagaceae to the Hamamelidae. Circumstantial evidence suggests abiotic dispersal is plesiomorphic in the Urticaceae and in the Moraceae/Cecropiaceae/Urticaceae complex: further evidence is required. Several results are note-worthy evolutionarily: (1) dispersal modes are malleable and can change within lineages; (2) this emphasizes the importance of mosaicism in angiosperm evolution; (3) the fossil and modern records suggest that families dominated by biotic dispersal are more diverse than families dominated by abiotic dispersal; (4) the Cretaceous-Tertiary boundary marks a time of major change in dispersal mode in the angiosperms; (5) the primitive fruit morphology of the Urticales appears to be the achene; and (6) derivation of fleshy structures from extra-ovarial tissues plays an important role in the dispersal of many species of the Moraceae, Cecropiaceae, and Urticaceae.

BACKGROUND AND HYPOTHESIS

The Hamamelidae are increasingly recognized as having been significant in the early history of the angiosperms. Members of the group have been traced to the Early Cretaceous (e.g., Doyle & Hickey, 1976; Hickey & Doyle, 1977) and in the earliest portions of the Late Cretaceous (Schwarzwalder & Dilcher, 1981); it is possible that the group may have had a separate origin from the Magnoliidae (Nixon, unpubl. data). Similarly, evidence for the importance and diversity of Hamamelidae in Cretaceous floras is growing. In particular, Leo Hickey (unpubl. data) has suggested, on the basis of fossil leaves, that the Hamamelidae reached a zenith of diversity in the Cretaceous and, with certain exceptions, have decreased in importance to the present day (see Cronquist, 1981: 153).

The fossil record of the angiosperms also reveals a pattern in relative sizes of diaspores. Cretaceous fruit and seed floras are dominated by small diaspores (1–3 mm on largest axis). Tertiary fruit and seed floras contain similarly small diaspores but also possess many much larger ones (Tiffney, 1984). As a broad generalization, small fruits and seeds may be abiotically or biotically dispersed, whereas large fruits and seeds are more often biotically dispersed. The small size of the Cretaceous angiosperm diaspores, together with the general absence of modern dispersal agents, suggests that Cretaceous angiosperms were largely abiotically dispersed. The extraordinary diversification of birds, bats, and terrestrial mammals in the early Tertiary (see Tiffney, 1984) provided biotic dispersal agents that are important in angiosperm biology today. These animals moved larger seeds than would abiotic means and were contributing factors to the evolution of modern angiosperms forming closed-canopy, late-successional forests such as those found in the warm-temperate and tropical areas of the world today (Tiffney, 1984). In sum, this scenario

suggests that Cretaceous angiosperm groups should be dominated by abiotic dispersal, and that biotic dispersal should be significant only in groups that either evolved in the Tertiary or altered their dispersal biology during that period.

If the assumption that the Hamamelidae are primarily a Cretaceous group is correct, then all "true" Hamamelidae should show fossil or recent evidence of abiotic dispersal. In theory, this provides one test of hypotheses on the systematic affinities of certain families [e.g., Juglandaceae (Hickey & Wolfe, 1975)] whose association with the Hamamelidae has been questioned. Families dominated by biotic dispersal mechanisms would presumably have affinities outside the Hamamelidae, whereas those with abiotic dispersal mechanisms are at least not disqualified from the sub-class. However, this conclusion rests on the further assumption that the primary dispersal mode within a family has not changed over time.

The reader is cautioned that, while focused on dispersal, this paper carries no implication that dispersal biology is more (or less) important than any other character in elucidation of the phylogeny of the Hamamelidae.

METHODS AND MATERIALS

In this paper, I follow Cronquist (1981) for disposition of families within the sub-class Hamamelidae and Willis (1973) for generic composition of the families.

Data on the modern modes of dispersal and associated information (Table 1) were assessed at the generic and occasionally the specific level, and were compiled from the following sources: Engler and Prantl (1894), Prain (1917), Standley (1920–1926, 1928), Engler and Prantl (1930), Ridley (1930), Standley and Steyermark (1946), Lawrence (1951), Martin et al. (1951), Standley and Steyermark (1952), Hutchinson and Dalziel (1954), Vink (1957), Jacobs (1960), Backer (1963), Hutchinson (1964), Melchior (1964), Owhi (1965), Hutchinson (1967), Radford et al. (1968), van der Pijl (1969), Miller (1971), Willis (1973), Walker (1976), Montgomery (1977), Soepadmo (1977), Croat (1978), Heywood (1978), Chang (1979), Kuang and Lu (1979), Li and Cheng (1979), Anonymous (1980), Elias (1980), Ming (1980), Wiggins (1980), Cronquist (1981), Dassanayake and Fosberg (1981). These sources are cited specifically only where warranted. In families possessing more than one dispersal mode, the relative contribution of the different modes

is expressed as a percentage of the total number of genera or species within the family. Cases in which dispersal mode is not recorded in the literature, or where it appeared equivocal or generalized in light of fruit or seed morphology, are noted individually.

The fossil record of angiosperm fruits and seeds is good in the Tertiary (Tiffney, 1977) but scanty in the Cretaceous. Only a few fruits and seeds of the Hamamelidae are known from the Cretaceous, although the record of the group is much better in the Tertiary. The appearance of modern dispersal agents roughly at the Cretaceous-Tertiary boundary presumably had a substantial effect on fruit and seed morphology, and may have influenced the appearance of "modern" characters. The absence of modern fruit and seed taxa in the Cretaceous may also partially be an artifact of scientific interest. Only within the last 15 years have researchers seriously examined Cretaceous angiosperm fruit and seed floras (e.g., Knobloch, 1971, 1977; Friis, 1983, pers. comm.; Knobloch & Mai, 1984; Tiffney, unpubl. data).

The fossil record of the families of the Hamamelidae is summarized in Figure 1. Figures 2–8 summarize the history of families with many genera reported from the fossil fruit and seed record. The data come from the primary literature and are taken from a file on the occurrences of fossil fruits and seeds that I have been assembling as a parallel to Muller's (1981) summary of the fossil pollen records of modern families.

The generic identifications are accepted as given by the primary authors. I have excluded some clearly erroneous reports but have not examined every occurrence in detail. In some cases this may be misleading. For example (Tiffney, in prep.), it may prove impossible to separate the seeds of many modern genera of the Hamamelidaceae in the fossil record. Thus, the reports of individual genera of Hamamelidaceae in Figure 2 may be misleading. Similarly, biases of preservation, mosaic evolution, and the attitudes of examining scientists may result in the placement of extinct forms in modern genera, or may cloud the recognition of modern genera in the fossil record.

Stratigraphic locations are taken as reported by primary authors except where clearly in error. Localities from western North America are dated from Evernden and James (1964) and Wolfe (1981). Period and Epoch durations are based on the time scale of Harland et al. (1982).

The summary of dispersal patterns in the fossil

TABLE 1. Characters of diversity, dispersal, distribution, habit, ecology, and pollination for the families of the Hamamelidae sensu Cronquist (1981). See text for sources.

Family	Number Genera/ Species	Genera Abiotically Dispersed	Dispersal Morphology	Genera Biotically Dispersed
Tetracentraceae (1)	1/1	100%	winged seed	0
Trochodendraceae (2)	1/1	100%	winged seed	0
Cercidiphyllaceae (3)	1/2	100%	winged seed	0
Eupteleaceae (4)	1/2	100%	winged fruit	0
Platanaceae (5)	1/6, 7	100%	hairy achene or nutlet	0
Hamamelidaceae (6)	28/100+	100%	winged seeds (18%) ballistic seeds (82%)	0
Myrothamnaceae (7)	1/2	100%	tiny seeds in capsule	0
Daphniphyllaceae (8)	1/35	0	fleshy drupe	100%
Didymelaceae (9)	1/2	0	large drupaceous fruit?	100%
Eucommiaceae (10)	1/1	100%	winged fruit	0
Barbeyaceae (11)	1/1	100%	nut with large accrescent se-pals	0
Ulmaceae (12)	18/150	33%	winged fruits and fleshy to semi-fleshy drupes	67%
Cannabaceae (13)	2/3	unclear—the bracts aid in wind dispersal, but Ridley (1930) records animal dispersal		
Moraceae (14)	51/1,333	8% genera (13% spp.)	dry achenes, some drupes, many pseudo-drupes	78% genera (86% spp.)
Cecropiaceae (15)	8/275	0	pseudo-drupes from fleshy floral parts	100%
Urticaceae (16)	46/1,255	37% genera (66% spp.)	abiotic via dry achene, ballistic, or winged fruit biotic via drupes, pseudo-berries, receptacle-fruit, sticky surfaces, and eliasomes	47.5% genera (29% spp.)
Leitneriaceae (17)	1/1	100% (?)	dry, possibly floating, drupe	0
Rhoipteleaceae (18)	1/1	100%	winged nut	0
Juglandaceae (19)	9/60	56% genera (37% spp.)	winged nut or drupaceous	44% genera (63% spp.)
Myricaceae (20)	3/50	unclear—no particular adaptations exist, and both abiotic and biotic dispersal observed		
Balanopaceae (21)	1/9	0	acorn-like drupe	100%
Fagaceae (22)	8/800	0	nut within cupule; rarely mildly winged	100%
Betulaceae (23)	6/120	83%	nut or samara	17%
Casuarinaceae (24)	1/50	100%	samaroid	0

TABLE 1. Continued.

| Distribution	Habit	Deciduous/ Evergreen	Dioecious/ Monoecious	Dispersal Unit	Pollination Mode
Nepal, China, Burma	tree	D	perfect	seed	anemophily
Korea, Japan, Taiwan	tree	E	androdioecious	seed	secondarily anemophily
China, Japan	tree	D	dioecious	seed	anemophily
China, Japan, Assam	tree	D	perfect to protandrous	fruit	anemophilous, some entomophily
Mediterranean to Himalayas, Assam; Mexico to Canada	tree	D	monoecious	fruit	anemophily
subtropical to temperate regions, Old and New Worlds	trees and shrubs	D & E	perfect or unisexual	seed	primarily entomophily
Africa, Madagascar	small shrub	?	dioecious	seed	anemophily
E Asia, Malaysia	trees or shrubs	?	dioecious	fruit	?
Madagascar	tree	E	dioecious	fruit	? anemophily
China	tree	D	dioecious	fruit	anemophily
NE Africa, Arabia	small tree	?	dioecious	fruit	anemophily
tropical and temperate Northern Hemisphere	trees, shrubs, and vines	D & E	monoecious or perfect	fruit	anemophily
N temperate to tropical	herbs	—	monoecious or dioecious	fruit	anemophily
widespread, largely tropical	trees, shrubs, and vines	D & E	monoecious or dioecious	fruit or "fruit" of floral parts	anemophily, some entomophily
tropical	trees, shrubs, and vines	?	rarely monoecious, commonly dioecious	fruit or "fruit" of floral parts	anemophily, some entomophily
tropical and subtropical, temperate	herbs, shrubs, vines, and trees (but mostly herbs)	—	monoecious, dioecious, and polygamous	fruit or "fruit" of floral parts	anemophily
SE United States	shrub to small tree	D	dioecious	fruit	anemophily
SW China, Vietnam	tree	D	perfect, sometimes unisexual	fruit	anemophily
Northern Hemisphere	trees	D	monoecious	fruit	anemophily
temperate and tropical, Old and New Worlds	shrubs	D & E	monoecious	fruit	anemophily
SW Pacific, New Caledonia	tree	E	dioecious	fruit	anemophily
cosmopolitan, except Africa	trees and shrubs	D & E	monoecious, seldom dioecious, rarely perfect	fruit	anemophilous, secondarily entomophilous in some species
temperate Northern Hemisphere	trees and shrubs	D	monoecious	fruit	anemophilous
SW Pacific, Australia, Indomalesia	trees and shrubs	E	monoecious	fruit	anemophilous
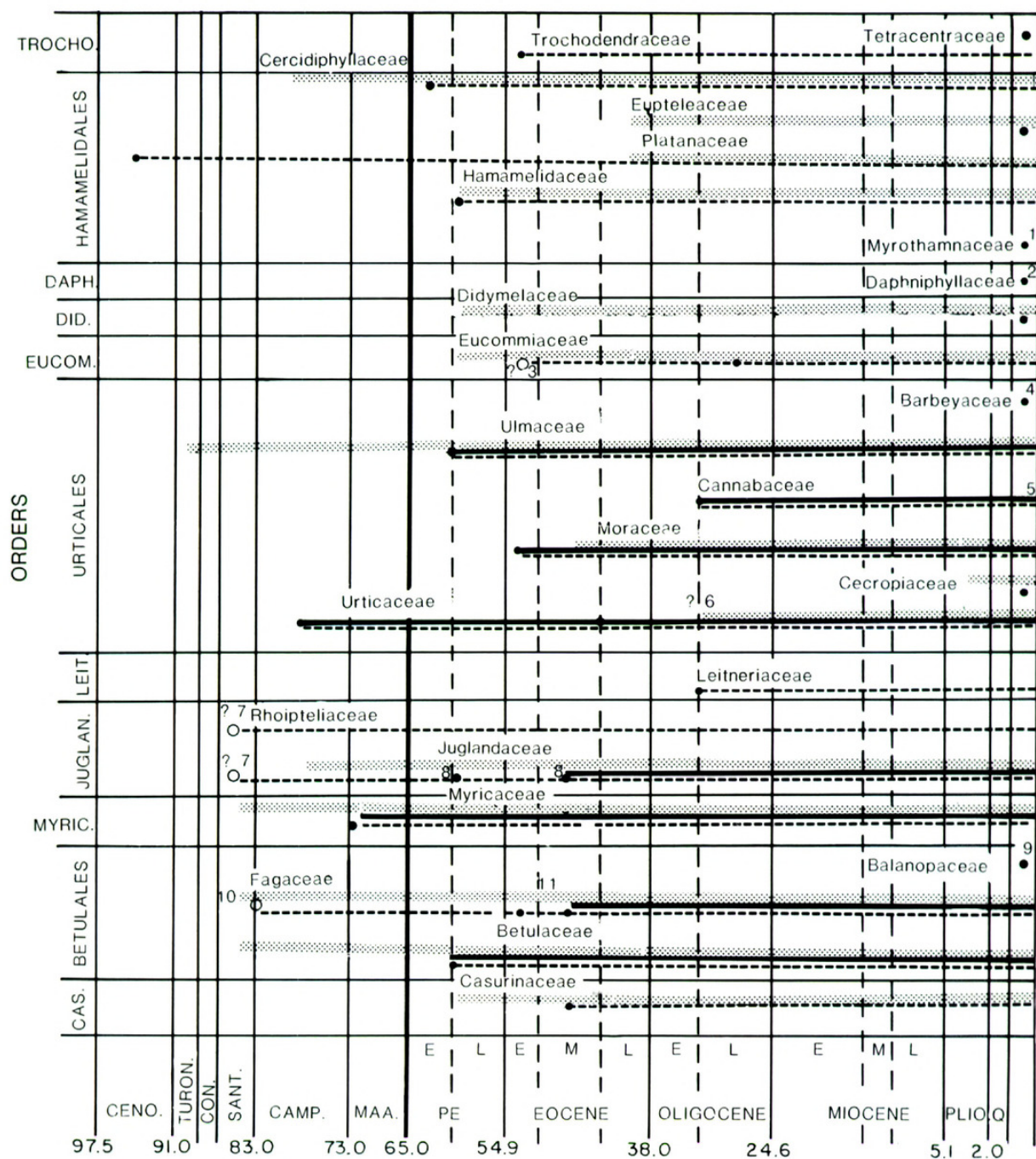
FIGURE 1.   First-occurrence data for families of the Hamamelidae sensu Cronquist (1981) based on fossil fruits, seeds, and pollen. Solid line, record of biotic dispersal within a family; dotted line, record of abiotic dispersal within a family; grey line, first occurrence data for pollen (after Muller, 1981). CENO. = Cenomanian, TURON. = Turonian, CON. = Coniacian, SANT. = Santonian, CAMP. = Campanian, MAA. = Maastrichtian, PE = Paleocene, PLIO = Pliocene, Q = Quaternary, E = Early, M = Middle, L = Late. Absolute dates after Harland et al. (1982). Trocho. = Trochodendrales, Daph. = Daphniphyllales, Did. = Didymelales, Eucom. = Eucommiales, Leit. = Leitneriales, Juglan. = Juglandales, Myric. = Myricales, Cas. = Casuarinales. Notes: (1) Abiotically dispersed; (2) Biotically dispersed; (3) *Eucommia*-like fruits of the early Eocene, Pierce and Hickey (pers. comm.); (4) Abiotically dispersed; (5) Cannabaceae appear to have "generalized" dispersal mechanisms; (6) Muller (1981) suggested possible Oligocene pollen of Urticaceae; (7) Friis (1983) reported fruits that conform most closely to those of the Juglandaceae but also possess similarities with those of the Myricaceae and Rhoipteleaceae; (8) *Casholdia, Polyptera,* and *Cyclocarya,* all wind dispersed, appear in the Upper Paleocene. The first animal-dispersed fruit of the family is *Juglans,* which appears in the Middle Eocene; (9) Biotically dispersed; (10) Tiffney and Friis have unpublished floral and fruiting material similar to Fagaceae from Martha's Vineyard, Massachusetts, United States. The identification requires verification; (11) *Fagopsis* (wind dispersed) appears in the Early Eocene; *Quercus* and possibly *Trigonobalanus* (animal dispersed) appear in the Middle Eocene.

record is based only on fossil fruit and seed records. Mosaic evolution (e.g., Manchester, 1981a; Knoll et al., 1984; Stebbins, 1984) dictates that it is inappropriate to infer a modern dispersal mechanism on the basis of a fossil leaf or pollen grain belonging to a modern genus. In these descriptions, when no reference is cited for a specific conclusion (e.g., that the morphology of the seeds of *Tetracentron* suggests abiotic dispersal), the conclusion is that of the present author.

RESULTS

Tetracentraceae. The fruit is a follicetum, dehiscing to release small seeds with spongy, wing-like outgrowths (Cronquist, 1981; Lawrence, 1951). The size and wings suggest abiotic dispersal.

Takhtajan (1974) placed Cretaceous specimens of *Nordenskioldia* Heer in the Trochodendrales, but there is no reason to accept these as members of either the Trochodendraceae or Tetracentraceae. The same reference also places *Nyssidium* Heer in the Trochodendrales, but Crane (1984a) demonstrated the affinities of many fossils assigned to this genus with the Cercidiphyllaceae (see below).

Trochodendraceae. The fruit is a follicetum, dehiscing to release many quite small seeds. The seed size suggests abiotic dispersal.

Reid and Chandler (1933) described *Trochodendron*(?) *pauciseminum* Reid & Chand. from the Early Eocene London Clay flora of England. The identification was given with a question mark, and is based on five- to six-loculed, septicidal fruits containing small seeds with (wing-like) extensions. If the identification is correct, then *Trochodendron* was abiotically dispersed in the Eocene.

Cercidiphyllaceae. The separate follicles bear small, asymmetrically-winged seeds. Wind dispersal is reported in the literature and borne out by personal observation.

The follicles of *Cercidiphyllum* are fairly common fossils (e.g., Brown, 1939; Jähnichen et al., 1980; Crane, 1984a). The oldest presently verified fruit record is from the Paleocene (Brown, 1962; Crane, 1984a). However, Crane (1984a) demonstrated that many fruits assigned to the form genus *Nyssidium* Heer represent the Cercidiphyllaceae, and reports of *Nyssidium* extend back to the Turonian (Takhtajan, 1974; see also Krasilov, 1976). Thus, fruits of the family could be present in the Late Cretaceous. It is likely that

the Cercidiphyllaceae were more diverse in the Late Cretaceous and early Tertiary. Crane and Stockey (1985) describe an extinct multi-organ assemblage as the genus *Joffrea* Crane & Stockey from Late Paleocene sediments: while varying in other characters, its seeds are very similar to those of *Cercidiphyllum*. Seeds found with fossil *Cercidiphyllum* follicles (Reid & Chandler, 1933; Crane, 1984a) resemble the seeds of the extant species, suggesting wind dispersal.

Eupteleaceae. The fruits are small samaras or winged nutlets adapted for wind dispersal. No fossil fruits are reported.

Platanaceae. The infructescence is a globose head of densely hairy achenes or nutlets that are shed at maturity. The hairs increase surface area, and the fruits may be wind dispersed or float on water.

Schwarzwalder and Dilcher (1981) described Cenomanian-age leaves and infructescences from Kansas that they suggest belong in the Platanaceae. Friis (1984) reported platanaceous inflorescences from the Late Cretaceous of North Carolina and Sweden. Hickey (pers. comm.) indicated that "*Platanus*-like" infructescences occur in the Lower Cretaceous sediments of the Potomac Group (see Hickey & Doyle, 1977). These records suggest that the Platanaceae are the oldest family of the Hamamelidae represented by fruiting remains. The morphology of the individual fruits is often similar to that of the fruits of modern *Platanus*, suggesting abiotic dispersal, although Manchester (1986) notes an Eocene *Platanus* with slightly larger fruits lacking the pappus-like hairs of the modern genus. These fruits are still quite small (2–3 mm) and Manchester (pers. comm.) suggests that they are probably abiotically dispersed.

Hamamelidaceae (Fig. 2). The majority of genera possess a ballistic dispersal mechanism in which the seed is "squirted" out from the fruit by pressures created in the fruit wall by moisture loss (e.g., *Hamamelis* L.). However, in the Altingioideae (*Altingia* Nor., *Liquidambar* L.) the seeds are very small and occasionally possess wings [although Vink (1957) noted that the oily seeds of *Altingia* have been observed to attract monkeys, birds, and ants]. Similarly, in the Hamamelidoideae, *Exbucklandia* R. W. Brown possesses large, winged seeds indicative of wind dispersal, and *Rhodoleia* Champ. ex Hook. has small, disk-like seeds dispersed by wind.

Both *Liquidambar* and the extinct genus *Steinhauera* Presl appear in the Paleocene (Chandler,
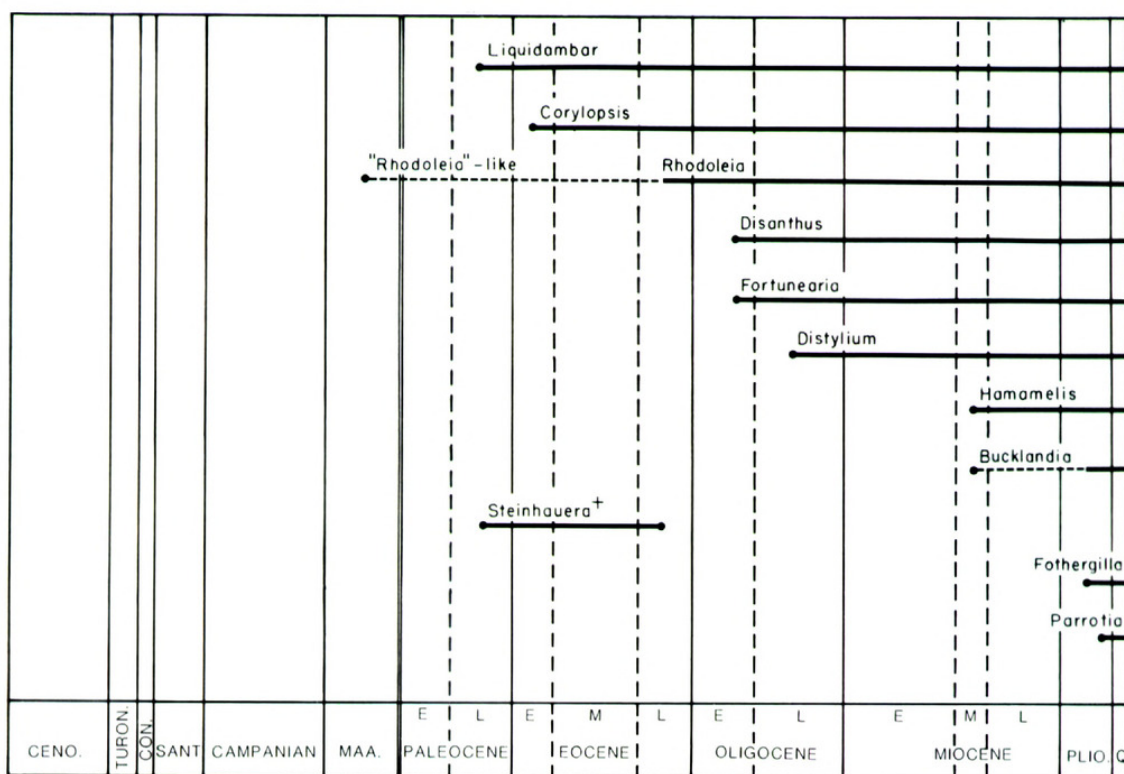
FIGURE 2. First-occurrence data for genera in the Hamamelidaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. *Liquidambar* L., Chandler (1961b); *Corylopsis* Sieb. & Zucc., Chandler (1961b); "*Rhodoleia*-like" (*Klikovispermum* Knob. & Mai), Knobloch and Mai (1984); *Rhodoleia* Champ., Mai and Walther (1985); *Disanthus* Maxim., Mai and Walther (1978); *Fortunearia* Rehdr. & Wils., Mai and Walther (1978); *Distylium* Sieb. & Zucc., Takhtajan (1974); *Hamamelis* L., Zablocki (1930); *Bucklandia* R. Br. ex Griff., first possible appearance, Brown (1946), later possible appearances, Reid and Reid (1915), Szafer (1946); *Fothergilla* L., Szafer (1946, 1954); *Parrotia* C. A. Mey., Tralau (1963); *Steinhauera* Presl, Mai (1968).

1961b; Mai, 1968; Collinson, unpubl. data). The shape of the fruits and seeds suggests wind dispersal. Knobloch and Mai (1984) drew a comparison between the fossil seed *Klikovispermum waltheri* Knobl. & Mai from the Maastrichtian of Czechoslovakia and the seeds of *Rhodoleia* Champ., but the first clear report of *Rhodoleia* is provided by Mai and Walther (1985) in the Late Eocene. Ballistically-dispersed members of the Hamamelidaceae first appear in the Early Eocene (*Corylopsis* Sieb. & Zucc., Chandler, 1961b), followed in the Oligocene by *Disanthus* Maxim., *Fortunearia* Rehder & Wilson (both reported by Mai & Walther, 1978), and *Distylium* Sieb. & Zucc. (Takhtajan, 1974). There is no evidence in the fossil record that the Hamamelidaceae were ever anything but wind or ballistically dispersed.

Myrothamnaceae. The fruit is a dehiscent capsule bearing many seeds (Cronquist, 1981), which Willis (1973) states are small. This suggests abiotic dispersal, but specific evidence is lacking. There is no fossil record of the fruits of the family.

Daphniphyllaceae. The fruit is a one-seeded, fleshy, indehiscent drupe that is black or green at maturity and about 1 cm long (Ridley, 1930; Walker, 1976; Cronquist, 1981). The fruit characters suggest biotic dispersal. There is no fossil record of the fruits of this family.

Didymelaceae. The fruit is "a large one-seeded drupe, with lateral grooves (as in *Prunus*)" (Willis, 1973). The morphology is suggestive of biotic dispersal. There is no fossil record of the fruits of this family.

Eucommiaceae. The fruit is a large samara, similar in shape to those of *Ailanthus* Desf. or *Fraxinus* L. Wind dispersal is indicated.

The oldest clear fossil is of *Eucommia krystofovichii* Negru from the Middle Miocene of Moldavia (Takhtajan, 1974). However, Brown (1940) reported samaras of *Eucommia montana* Brown from the ? Upper Oligocene of western North America (see note under Ulmaceae). The
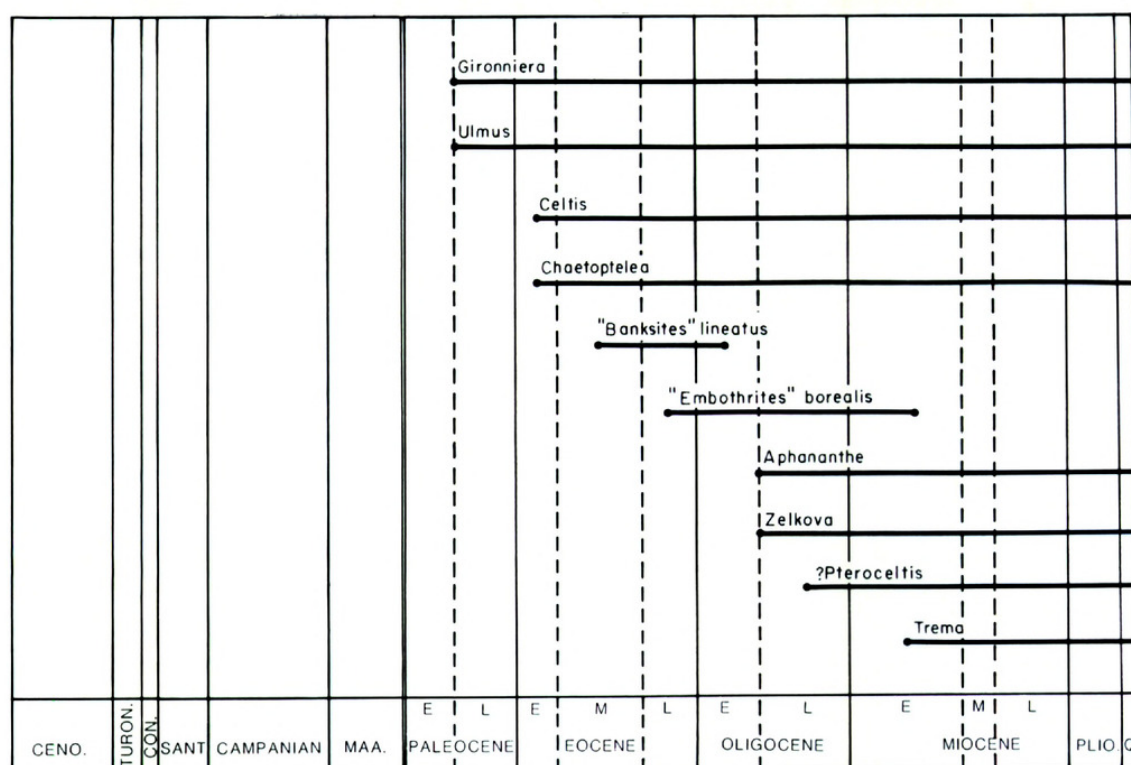
FIGURE 3. First-occurrence data for genera in the Ulmaceae based on fossil fruits and seeds. Conventions as in Figure 1. *Gironniera* Gaudich., unpublished data cited in Mai and Gregor (1982); *Ulmus* L., first report Brown (1962), next report Givulescu (1980); *Celtis* L., unpublished specimens provided by Leo J. Hickey; *Chaetoptelea* Liebm., MacGinitie (1941); "*Banksites*" *lineatus* Unger, Manchester (in prep.); *Embothrites borealis* Unger, Manchester (in prep.); *Aphananthe* Planch., Takhtajan (1982); *Zelkova* Spach., Chandler (1957); ? *Ptero-celtis* Maxim., first report Weyland (1937), questioned by Kirchheimer (1957); *Trema* Lour., Holý (1975).

latter fruits are shorter and broader than those of modern *Eucommia* and might constitute an extinct genus. Similarly, Pierce and Hickey (pers. comm.) are investigating a samara from the Paleocene of western North America that is similar to the fruits of the modern genus but differs in several specifics. The last two reports hint at a greater taxonomic diversity in the family in the early Tertiary and underscore the importance of wind dispersal in the group.

Barbeyaceae. The fruit is a "short-beaked nut with associated accrescent, somewhat membranous, prominently veined sepals" (Cronquist, 1981). In some species the length of the sepals exceeds that of the nut by 2:1 (Prain, 1917). These morphological characters suggest wind dispersal, although animal predation and dispersal of the nut could not be excluded. There is no fossil record of the fruits of this family.

Ulmaceae (Fig. 3). The Ulmoideae (five genera) possess wind-dispersed samaras, with the exception of *Planera* J. F. Gmel, which has a fleshy fruit. The Celtidoideae (ca. 12 genera) pos-

sess fleshy-walled, animal-dispersed, drupes with the exception of *Pteroceltis* Maxim., which has a winged fruit, and *Chaetacme* Planch., which has a tiny, hard-surfaced drupe (Hutchinson, 1967). Twenty-six percent of the species of the family are abiotically-dispersed samaras and 74% are drupes presumed to be biotically dispersed.

Fruits of the two subfamilies appear in the fossil record at approximately the same time. The Ulmoideae are first represented by *Ulmus* L., which appears in the Paleocene of western North America (Brown, 1962), although this record may include some material of *Eucommia* (P. Crane, pers. comm.). *Chaetoptelea* Liebm. appears in the Early Eocene of western North America (MacGinitie, 1941), and the extinct form "*Banksites*" *lineatus* Unger appears in the Middle Eocene of the same area, persisting to the Early Oligocene (Manchester, in prep.). The extinct form "*Embothrites borealis*" Unger appears in the Upper Eocene of Europe and persists through the Early Miocene (Manchester, in prep.).

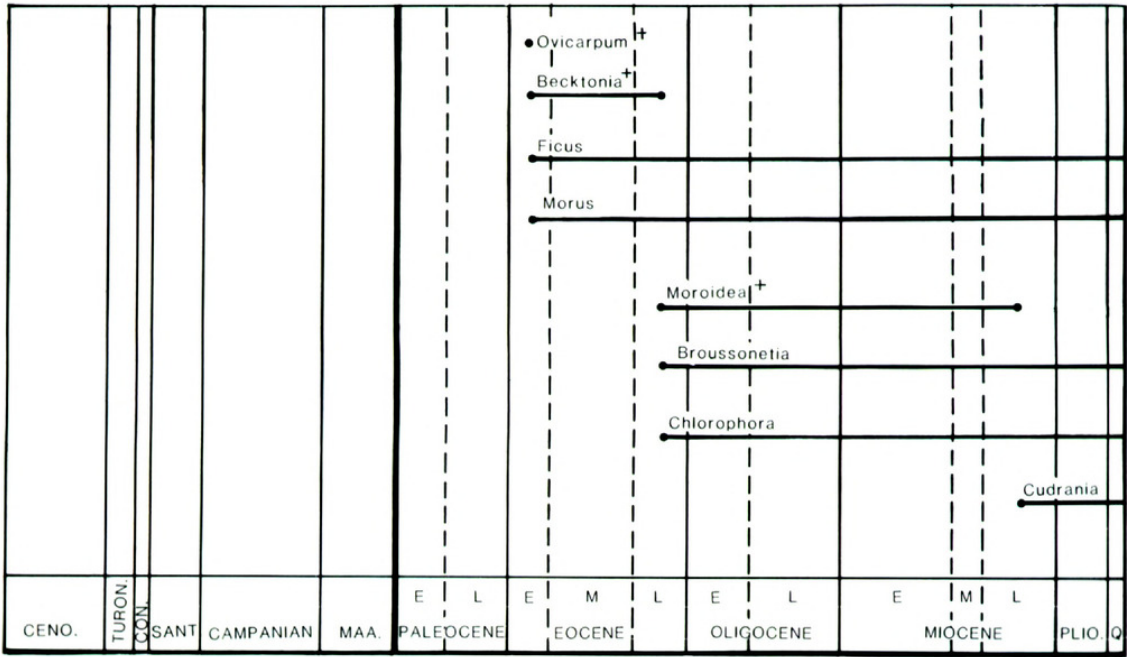The Celtidoideae are first represented by en-

FIGURE 4. First-occurrence data for genera in the Moraceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. *Ovicarpum* Chandler, Chandler (1962); *Becktonia* Chandler, first report Chandler (1963), last report Chandler (1961a); *Ficus* L., Chandler (1962); *Morus* L., Chandler (1961b); *Moroidea* Chandler, first report Chandler (1961a), last report Palamarev (1971); *Broussonetia* L'Hérit. ex Vent., Chandler (1925–1926, 1961a); *Chlorophora* Gaudich., Chandler (1925–1926, 1961a); *Cudrania* Trécul, Palamarev (1968).

docarps of *Gironniera* Gaudich., in the Paleocene of Europe (unpubl. data cited in Mai & Gregor, 1982). This is closely followed by endocarps of *Celtis* L. from the Early Eocene of western North America (Leo Hickey, pers. comm.). Only one more genus of the Ulmoideae appears, this in the Oligocene, compared to three more of the Celtidoideae; possibly two in the Oligocene and one in the Miocene. [Weyland's (1937) report of *Petroceltis* Maxim. has been questioned by Kirchheimer (1957).] This imbalance of subsequent appearances could be taken to reflect differential diversification of the two subfamilies; the Celtidoideae are more numerous in the present day.

Cannabaceae. The fruit is an achene invested to a greater or lesser degree in a persistent calyx. If large enough, the calyx wings permit wind dispersal in *Humulus* L., but often the wings are reduced and wind dispersal is impossible (Ridley, 1930). Animal dispersal is known in *Cannabis* L. (Ridley, 1930) and may be significant. Neither dispersal mechanism is dominant in either genus.

Dorofeev (in Takhtajan, 1982) reported four species of *Humulus* L. and two species of the extinct genus *Humularia* Dorof. [which requires a new name, as *Humularia* Duvign. (Leguminosae) has nomenclatural priority] as appearing in the Oligocene of western Siberia. The first re-

port of *Cannabis* L. is in the Miocene of eastern Siberia (Dorofeev, 1969). The morphology of the fruits suggests no particular change from their present "generalized" dispersal adaptations.

Moraceae (Fig. 4). Out of 51 genera of Moraceae examined, 78% had fleshy diaspores and 8% had dry, presumably abiotically-dispersed fruits. I was unable to ascertain fruit type in 14%. At the species level, 86% of the diaspores are fleshy and 13% are dry. Based on the total sample of the fleshy-diaspore genera, only 11% are drupes (true fruits in which flesh is derived from the carpel wall), whereas over 67% are dispersal structures in which the flesh is provided by enlarged, accrescent floral parts or enlarged receptacles surrounding an achene. This pattern is clearer at the species level, where almost all fleshy diaspores are derived from perianth parts. Thus, although biotic dispersal adaptations strongly dominate in the Moraceae, the attractive diaspore structure does not develop from the true fruit, but from structures external to it. Floral parts also participate in abiotic dispersal. Ridley (1930) noted in *Sloetia sideroxylon* Teijsm. & Binneud ex Kurz. that the swollen sepals may squeeze the mature achene out of the floral remains with enough force to throw the achene a yard. In *Dorstenia* L., Ridley noted that drying of the receptacle and enclosed flowers creates
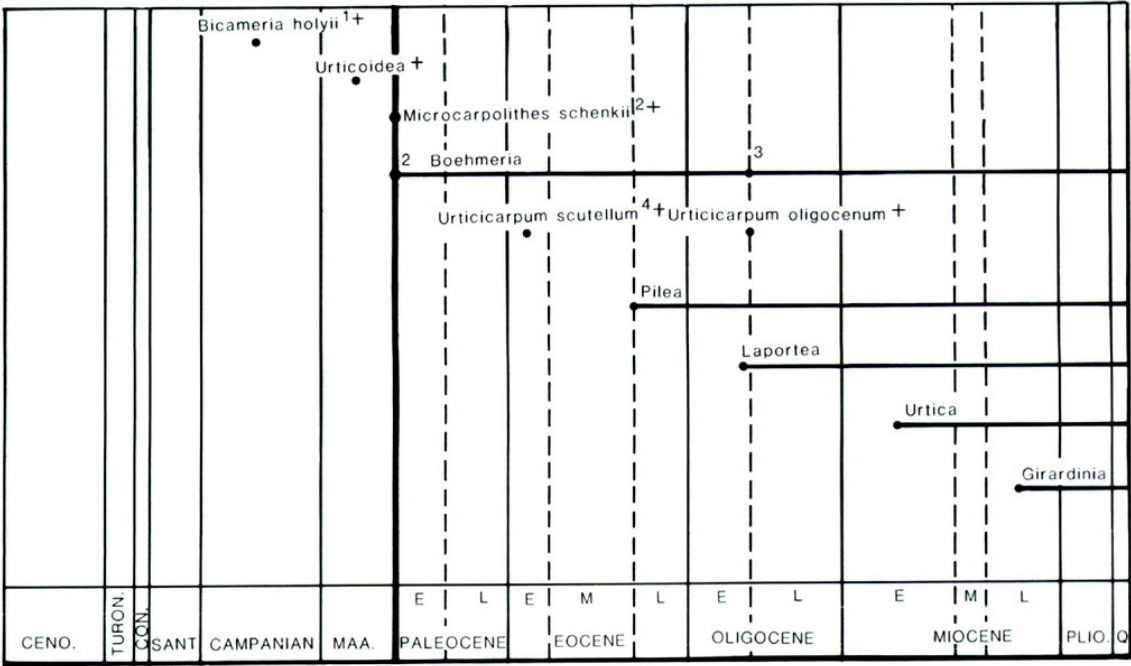
FIGURE 5.　First-occurrence data for genera in the Urticaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. Notes: (1) "Senonian" age assigned, this encompasses stages ranging from the Coniacian to Maastrichtian; (2) age given as Maastrichtian to Paleocene; (3) next report of *Boehmeria*, Takhtajan (1982); (4) affinities with the Urticaceae uncertain, *Bicameria holyii* Knobloch & Mai, Knobloch and Mai (1984); *Urticoidea* Knobloch & Mai, Knobloch and Mai (1984); *Microcarpolithes schenkii* Knobloch, Knobloch (1971); *Boehmeria* Jacq., Knobloch (1971); *Urticicarpum scutellum* Reid & Chandler, Reid and Chandler (1933); *Urticicarpum oligocenum* Dorof., Dorofeev (in Takhtajan, 1982); *Pilea* Lindl., Palamarev (1973); *Laportea* Gaudich., Mai and Walther (1978); *Urtica* L., Dorofeev (in Takhtajan, 1982); *Girardinia* Gaudich., Dorofeev (in Takhtajan, 1982).

enough pressure to "shoot" the achenes away from the plant.

Fig-like objects (*Ficus ceratops* Knowl.) have been reported from the Late Cretaceous of western North America but lack the internal structure and external morphologic detail necessary for secure systematic assignment. Shoemaker (1977) reviewed these fossils and placed them in the form genus *Carpites* Schimper. The first assured occurrence of this family is in the Early Eocene floras of southern England, where *Ficus* L. (Chandler, 1962), *Morus* L. (Chandler, 1961b), and two extinct genera, *Ovicarpum* Chandl. (Chandler, 1962) and *Becktonia* Chandl. (Chandler, 1963) are reported. This is followed by the appearance of *Broussonetia* L'Hérit ex Vent., *Chlorophora* Gaudich., and the extinct genus *Moroidea* Chandl. (all Chandler, 1961a) in the Late Eocene. These fossils largely are of achenes that could have been borne within a fleshy berry of the involucre or could have been dispersed dry. If one accepts the identifications of the modern genera (*Ficus, Morus, Broussonetia, Chlorophora*) as correct, biotic dispersal was dominant in the family from its first appearance.

Cecropiaceae.　All eight genera possess fleshy diaspores indicative of animal dispersal. Similar to the Moraceae, the flesh in these diaspores is primarily derived from floral parts, rather than from the carpel wall. There is no fossil record of the fruits or seeds of this family.

Urticaceae (Fig. 5).　As in the Moraceae, the basic fruit type is an achene, a small nut or rarely a drupe, and the floral parts play a strong role in dispersal. However, abiotic dispersal is common in this family; out of 46 genera, over 47% are biotically dispersed, about 37% abiotically dispersed, and data could not be obtained for 15%. The pattern is inverted at the species level. Almost 66% of the species are abiotically dispersed, over 29% biotically, and almost 5% unknown. Of the abiotically-dispersed genera, roughly half had mechanisms developed from the true fruit, whereas the other half had mechanisms dependent on accrescent floral parts forming wings, hairs, or aiding in ballistic dispersal. Of the biotically-dispersed genera, well over half are berry-mimics based on fleshy floral parts and one-third have sticky or hairy floral parts that are assumed to attach the fruit to animals. In one genus, the

floral parts appear to form an eliasome-mimic that attracts ants. Only three genera of animal-dispersed forms have true drupes.

The fossil record of the Urticaceae is "bipartite," with a cluster of largely extinct genera of fruits from the Cretaceous and early Tertiary, followed by the appearance of modern genera of fruits in the Oligocene. Knobloch and Mai (1984) relate *Bicameria holyi* Knobl. & Mai of the Senonian and *Urticoidea cucurbitoides* Knobl. & Mai of the Maastrichtian to the family, and Knobloch (1971) described *Microcarpolithes schenkii* Knobl. and *Boehmeria ctyrokyi* Knobl. from undifferentiated sediments ranging from Campanian to Paleocene in age. If the last identification is correct, then it is the oldest report of a modern genus in the group. If not, then the first is *Pilea* Lindl., which appears in the Upper Eocene (Palamarev, 1973), followed by *Boehmeria* Jacq. (Takhtajan, 1982), and *Laportea* Gaudich. (Mai & Walther, 1978) in the mid-Oligocene. As with the Moraceae, it is not possible to infer mode of dispersal from the morphology of the fruits. If one follows the dispersal modes of the modern genera in the fossil record (*Boehmeria, Pilea, Laportea, Urtica*), they are abiotically dispersed with the exception of *Boehmeria*.

Leitneriaceae. The fruit is a dry drupe with a leathery, slightly spongy exocarp. This could facilitate animal dispersal or, in light of the moist habitats in which *Leitneria* Chapm. grows, possibly aid in water dispersal.

Dorofeev (1963; recent stratigraphy from Takhtajan, 1982) reported *Leitneria venosa* (Ludwig) Dorof. from several Oligocene localities in western Siberia. No difference in dispersal mechanisms from the extant *L. floridana* Chapman can be inferred from the fossil.

Rhoipteleaceae. The two-winged samaroid nut is wind dispersed. See discussion under Juglandaceae for fossil record.

Juglandaceae (Fig. 6). The fruit is a nut, which may either be samaroid or drupaceous, corresponding to wind or animal dispersal. By species number, the drupaceous forms (*Carya* Nutt. and *Juglans* L.) outnumber the wind-dispersed ones about 2:1. Further details of dispersal in this family are provided in the section on the alteration of dispersal mode within families.

The oldest records of fruits with possible juglandalean affinity are of the form genera *Manningia* Friis, *Antiquocarya* Friis, and *Caryanthus*

Friis from the Senonian of Sweden. While these flowers and fruits differ from those of extant Juglandaceae in some characters and in their size, and while they may be compared to modern flowers and fruits of the Myricaceae and Rhoipteleaceae in some respects, Friis (1983: 185–186) concluded "the best correlation of the fossil fruits and floral structures described here is with members of the Juglandaceae." Given this evidence, it seems best to recognize the fossils as closely associated with the precursors of modern Juglandaceae, if not actually representative of the family.

Cyclocarya Iljinskaja co-occurs in the upper Paleocene with the extinct genera *Polyptera* Manchester & Dilcher (both Manchester & Dilcher, 1982), *Casholdia* Crane & Manchester (Crane & Manchester, 1982), and the form genus *Juglandicarya* Reid & Chandler (Manchester, 1981a); all but the last-named are winged. This is followed by the appearance of the winged genera *Englehardtia* Leschen. ex Bl. (Jähnichen et al., 1977; Manchester, 1981a), *Platycarya* Sieb. & Zucc. (Chandler, 1964; Wing & Hickey, 1984), and *Pterocarya* Kunth. (Manchester & Dilcher, 1982) in the Early Eocene. The animal dispersed *Juglans* L. appears in the Middle Eocene (Manchester, 1981a), and *Carya* Nutt. appears at the Eocene-Oligocene border (Mai, 1981).

The Senonian fruits are quite small and show no sign of fleshy exocarps; features suggestive of abiotic dispersal. There is a clear transition in numerical dominance from wind-dispersed species to animal-dispersed species through the Tertiary (see Fig. 9 and discussion below).

Myricaceae. The fruit is drupaceous or almost a nutlet, sometimes enclosed by small bracteoles. As with the Cannabaceae, it is difficult to reach a satisfactory generalization about dispersal in the family. Ridley (1930) and Martin et al. (1951) noted that the fruits are dispersed by birds, but water and wind dispersal are also possible. In light of these observations, no single dispersal mode is assumed for this family.

The earliest report is of *Comptonia octocostata* (Knobl.) Knobl. from the early Maastrichtian of Europe (Knobloch, 1975; Jung et al., 1978). This is followed by *C. goniocarpa* Mai & Walther from the Early to mid-Oligocene of East Germany (Mai & Walther, 1978). *Myrica boveyana* (Heer) Chandl. appears in the Early Eocene of southern England (Chandler, 1961b) and is followed by a host of subsequent reports of other species. The
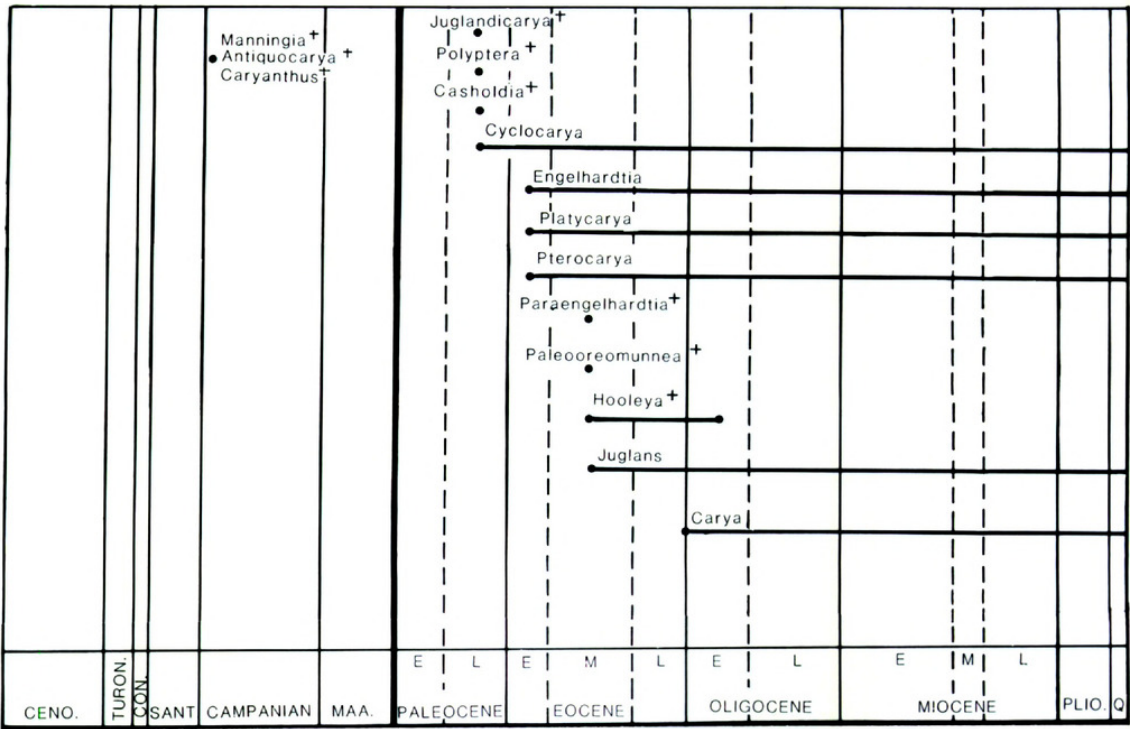
FIGURE 6. First-occurrence data for genera in the Juglandaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. Although published sources of first occurrences are given, much insight comes from Manchester (1981a). *Manningia* Friis; *Antiquocarya* Friis; *Caryanthus* Friis, Friis (1983); *Juglandicarya* Reid & Chandler, Reid and Chandler (1933), Manchester (1981a); *Polyptera* Manchester & Dilcher, Manchester and Dilcher (1982); *Casholdia* Crane & Manchester, Crane and Manchester (1982); *Cyclocarya* Iljinskaja, Manchester and Dilcher (1982); *Engelhardtia* Leschen. ex Bl., Jähnichen et al. (1977), Manchester (1981a, note: Manchester placed all fossil Engelhardtioid fruits into the form genus *Palaeocarya* Saporta, as the range of variation seen in the fossils exceeds that in the modern genus sensu stricto. I retain *Engelhardtia* here as a more familiar concept, accepting that it may encompass several genera); *Platycarya* Sieb. & Zucc., Chandler (1964), Wing and Hickey (1984); *Pterocarya* Kunth, Manchester and Dilcher (1982); *Paraengelhardia* Berry, Dilcher et al. (1976); *Paleooreomunnea* Dilcher, Potter & Crepet, Dilcher et al. (1976); *Hooleya* Reid & Chandler, Wing and Hickey (1984); *Juglans* L., Brown (1962), Manchester (1981b); *Carya* Nutt., Mai (1981).

morphology of the fossils parallels that of the living species, suggesting a similar "generalized" dispersal syndrome in the past.

Balanopaceae. The fruit is a fleshy-walled, acorn-like drupe, sitting in an acorn-like cup (Willis, 1973; Cronquist, 1981). The fruit morphology suggests biotic dispersal. There is no fossil record of the fruits of this family.

Fagaceae (Fig. 7). The fruits are nuts, often of considerable size, indicating biotic dispersal. Only in *Nothofagus* Blume are samaroid fruits occasionally encountered, although Soepadmo (1977) noted that, in most species, they are large and disperse very poorly. The family may be considered biotically dispersed.

The oldest fruit of the family may be represented by reproductive material from the Santonian-Campanian of Massachusetts, United States. These most closely resemble miniaturized fruits of *Lithocarpus* Bl. in morphology (Tiffney

& Friis, unpubl. data). This record requires validation. The extinct genus *Fagopsis* Hollick appears in the Early Eocene (Manchester & Crane, 1983), followed by *Trigonobalanus* Forman (Mai & Walther, 1978), *Quercus* L. (Bones, 1979; Manchester, 1981b), and possibly *Castanea* Mill. (Crepet & Daghlian, 1980) in the Middle Eocene. *Lithocarpus* Bl. may appear in the Late Eocene (Axelrod, 1966), although Manchester and Crane (1983) are dubious of this record. *Fagus* L. appears in both Europe (Chandler, 1957) and North America (Chaney, 1927; supported by Smiley & Huggins, 1981) in the mid-Oligocene.

The Cretaceous fossils are about 3 mm in diameter, show no signs of a fleshy covering, and occur in prodigious numbers, all suggestive of abiotic dispersal. *Fagopsis* is the earliest known Tertiary representative of the group and produces small fruits borne within wing-like cupules, often aggregated in rings, the whole ap-
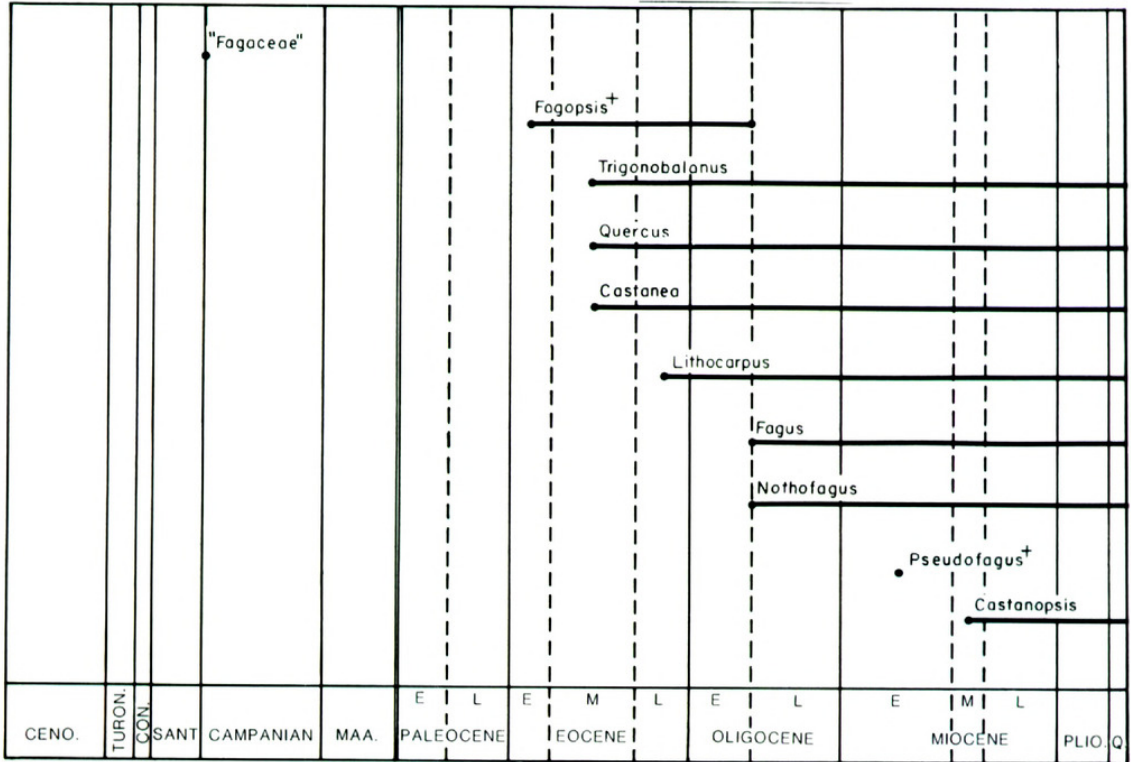
FIGURE 7. First-occurrence data for genera in the Fagaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. "Fagaceae," possible fagaceous flowers and fruits under investigation by Tiffney and Friis; *Fagopsis* Hollick, Manchester and Crane (1983); *Trigonobalanus* Forman, Mai and Walther (1978); *Quercus* L., Manchester (1981b); *Castanea* Mill., Crepet and Daghlian (1980); *Lithocarpus* Bl., Axelrod (1966), see Manchester and Crane (1983); *Fagus* L., Chaney (1927), Chandler (1957); *Nothofagus* L., Hill (1983); *Pseudofagus* Smiley & Huggins, Smiley and Huggins (1981); *Castanopsis* (D. Don) Spach., Mai (1964); *Castanea* Mill., van der Burgh (1978).

parently adapted for wind dispersal. The other members of the family, including the extinct mid-Tertiary *Pseudofagus idahoensis* Smiley & Huggins (Smiley & Huggins, 1981), are animal dispersed.

Betulaceae (Fig. 8). Of the six living genera, the fruits of *Alnus* Mill. and *Betula* L. are wind dispersed. *Carpinus* L. and *Ostrya* Scop. fruits may be wind dispersed [Ridley (1930) gave evidence that they travel respectable distances], or the bracts may be too small to permit effective dispersal. Thus, animal dispersal may also be important in these genera (Ridley, 1930; Martin et al., 1951). *Corylus* L. generally has a nut too large to be wind-borne by its bracts and is often animal dispersed (Ridley, 1930). The dispersal mode in *Ostryopsis* Decne. is not reported in the literature. Illustrations of the fruit (Li & Cheng, 1979) show a relatively large fruit in a winged involucre. In sum, dispersal mechanisms intergrade from animal to wind in the family.

The oldest fossil records involve *Corylus* L.

(Brown, 1962; Koch, 1978) from North America and Greenland and the extinct genus *Palaeocarpinus* Crane (Crane, 1981) from England and North America (Crane, 1984b), both appearing in the mid-Paleocene. In addition, Crane (1981) suggests that "*Atriplex*" *borealis* (Heer) Laurent of the Paleocene may also belong to the family. *Alnus* Mill. appears at the Paleocene/Eocene boundary (Takhtajan, 1982) and *Betula* L. in the Middle Eocene (Crane, 1984b). *Carpinus* L. may appear in the Late Paleocene (Chandler, 1961b), although Crane (pers. comm.) believes this record is of *Palaeocarpinus,* and that the first fossil fruit of *Carpinus* is of Late Eocene age (see Crane, 1981). With the exception of *Corylus,* all fossil members of the family are morphologically adapted to a greater or lesser degree for wind dispersal.

Casuarinaceae. The seed is a small, one-seeded samara, well-adapted for wind dispersal. Christophel (1980) reported mature inflorescences of *Casuarina* Adans. from the Eocene of
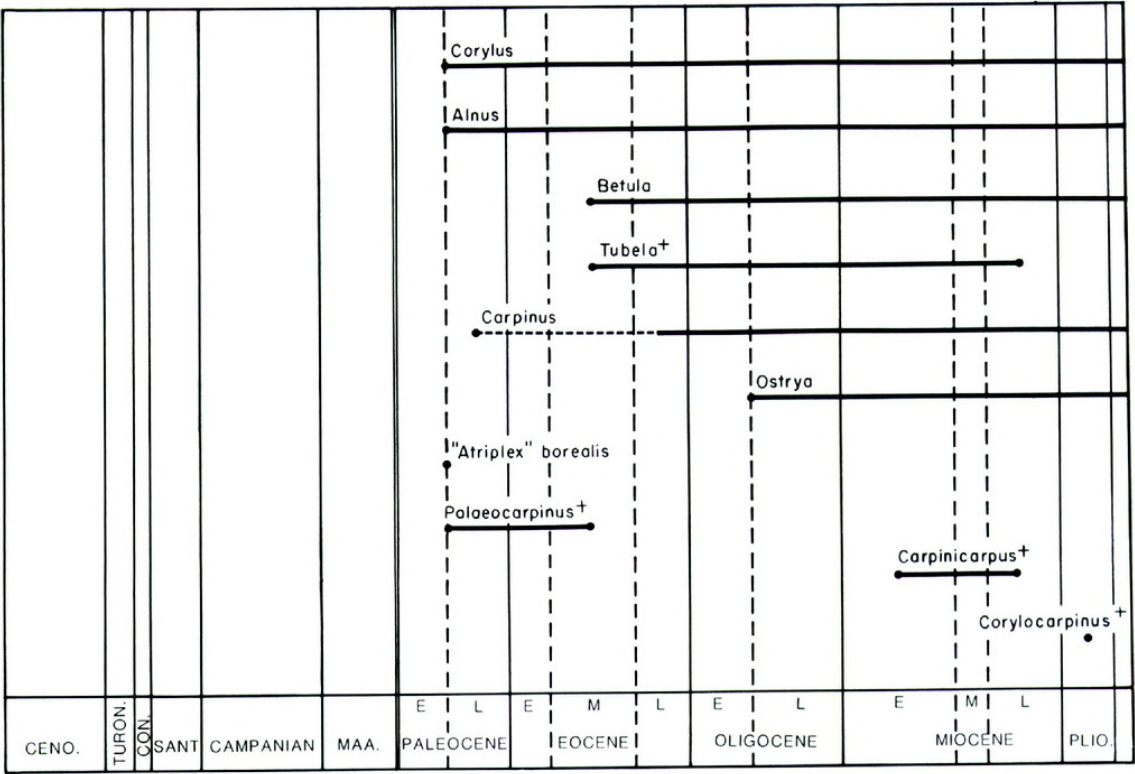
FIGURE 8.   First-occurrence data for genera in the Betulaceae based on fossil fruits and seeds. Conventions as in Figure 1, + indicates extinct genus. *Corylus* L., Brown (1962), Koch (1978); *Alnus* Mill., P. Crane, (pers. comm.), first published report from Paleocene-Eocene border, Dorofeev (in Takhtajan, 1982); *Carpinus* L., Chandler (1961b), P. Crane (pers. comm.) suggested this may be *Palaeocarpinus* and that the earliest *Carpinus* fruit is Late Eocene; *Betula* L., Dorofeev (in Takhtajan, 1982); *Tubela* Dorof., Dorofeev (in Takhtajan, 1982); *Ostrya* Scop., Dorofeev (in Takhtajan, 1982); "*Atriplex*" *borealis* (Heer) Laurent, Crane (1981); *Palaeocarpinus* Crane, Crane (1981), Crane and Stockey (1986); *Carpinicarpus* Nikitin, Nikitin (1965); *Corylocarpinus* Straus, Straus (1969).

Australia that are virtually identical to those of modern species. This suggests that the Eocene members were also wind dispersed.

SUMMARY OF ABIOTICALLY-DISPERSED FAMILIES

The Trochodendraceae, Cercidiphyllaceae, Platanaceae, Myrothamnaceae, Eucommiaceae, Barbeyaceae, Rhoipteleaceae, and Casuarinaceae are dominated in the present day by forms with winged or very small fruits or seeds adapted for wind dispersal. The Hamamelidaceae have a few taxa that are wind dispersed, but the majority are ballistically dispersed. Where the above families are known in the fossil record, they are abiotically dispersed.

SUMMARY OF INTERMEDIATE FAMILIES

The Cannabaceae and Myricaceae possess fruits that are often enveloped in bracteoles. The fruits could float or be wind dispersed. The often spiny *Comptonia* bracteoles might adhere to animals. The fruits of these groups could also be eaten and dispersed. The fruit of the Leitneriaceae could equally well attract animal dispersers or float. The fossil records of the Cannabaceae, Myricaceae, and Leitneriaceae indicate no change in morphology of the fruit in the recorded past. The Ulmaceae possess approximately 25% abiotically-dispersed, and 75% animal-dispersed, species. The fossil record indicates that both dispersal modes appeared simultaneously, but that animal dispersal may have become more important during the Tertiary. Two-thirds of the species of the Urticaceae are abiotically dispersed, whereas 30% are animal dispersed. The fossil record of urticaceous fruits does not clearly indicate the nature of dispersal in the past. In the extant Juglandaceae, 63% of the species are biotically dispersed and 37% are abiotically dispersed. Senonian fruits of juglandalean affinity

are probably abiotically dispersed. Whereas both wind- and animal-dispersed fruits are present in the early Tertiary, there is a clear rise in dominance of biotically-dispersed species through the Tertiary (Fig. 9). Three genera of extant Betulaceae are wind dispersed, two can be wind or animal dispersed, and *Corylus* is animal dispersed. Abiotically- and biotically-dispersed betulaceous diaspores appear simultaneously in the fossil record.

SUMMARY OF BIOTICALLY-DISPERSED FAMILIES

The Daphniphyllaceae, Didymelaceae, and Balanopaceae possess fleshy fruits suggestive of animal dispersal; they all lack fossil records. The Moraceae are almost entirely animal dispersed today. The fossil record is possibly equivocal but could be read to show no evidence of abiotic dispersal. The Cecropiaceae are entirely biotically dispersed today and lack a fossil record. The Fagaceae are almost, if not entirely, biotically dispersed in the present day. Possible middle Late Cretaceous fagaceous fruits are abiotically dispersed. The next genus to appear in the fossil record of the family (*Fagopsis*) is wind dispersed. All others are animal dispersed.

DISCUSSION

BIOTIC DISPERSAL AND PHYLOGENY

At the outset, I outlined two assumptions; that the Hamamelidae reached a zenith in the Cretaceous and are largely a relict group today, and that abiotic dispersal is primitive in angiosperms. Given these premises, logic suggests that families dominated by biotic dispersal and included in the Hamamelidae may be mis-allied with the sub-class.

Biotic dispersal is important in three orders of the Hamamelidae; the Urticales (Ulmaceae, Moraceae, Cecropiaceae, Urticaceae), the Juglandales (Juglandaceae and Balanopaceae), and Fagales (Fagaceae and a small portion of the Betulaceae). In addition, it dominates the Daphniphyllaceae and Didymelaceae. With the exception of the last two small "outliers," all of the groups mentioned lie among the "advanced" Hamamelidae, and questions have been raised about the proper placement of all of these groups.

The Urticales have been allied with the Malvales (Dilleniidae) rather than with the Hamamelidae (e.g., Thorne, 1973; Berg, 1977), a so-

lution perhaps borne out by leaf architecture (Leo Hickey, pers. comm.). However, separate evidence suggests assignment to the Hamamelidae (Cronquist, 1981: 186). The Juglandales have long been a bone of phylogenetic contention, with alternative views allying them with the Hamamelidae or the Rosidae [near Anacardiaceae (Sapindales)]. The dominance of biotic dispersal in modern representatives of the family would appear to support features of leaf architecture (e.g., Hickey & Wolfe, 1975) in arguing for their Rosid affinity. Again, however, there is much evidence for their association with the Hamamelidae (Cronquist, 1981: 204–207). The Fagales are not generally contested as Hamamelids, although Hickey and Wolfe (1975) did note that the leaf architectural affinities of the order (excluding Balanopales and Betulales) were "uncertain." Of the smaller families in question, Hickey and Wolfe (1975) transferred the Didymelaceae to the Dilleniidae and Thorne (1976) referred it to the Euphorbiales (both paralleling its biotic dispersal), but Cronquist (1981) considered it most harmoniously placed in the Hamamelidae. The Daphniphyllaceae are another taxonomic football, alternating between placement in the Euphorbiaceae (Rosidae) and the Hamamelidae (see Cronquist, 1981), but without resolution. Here the biotic dispersal would join evidence for a euphorbian alliance.

In summary, dispersal evidence would appear to support arguments for exclusion of the Juglandales, Didymelaceae, Daphniphyllaceae, and several families of the Urticales from the Hamamelidae and raises questions about the association of the Fagales with the sub-class. However, acceptance of these conclusions based on modern dispersal modes assumes that the families in question have not altered their primary mode of dispersal over time. The diversification of important groups of modern dispersal agents in the early Tertiary indicates that plant lineages dating from the Late Cretaceous or Tertiary (e.g., Juglandaceae, Fagaceae, Urticaceae) may have passed through a period of intense selective pressure involving changing dispersal mechanisms (Tiffney, 1984).

EVIDENCE FOR ALTERATION OF DISPERSAL MODE WITHIN A FAMILY

Two, possibly three, examples in the fossil record and one from modern evidence suggest that the dominant mode of dispersal changed over
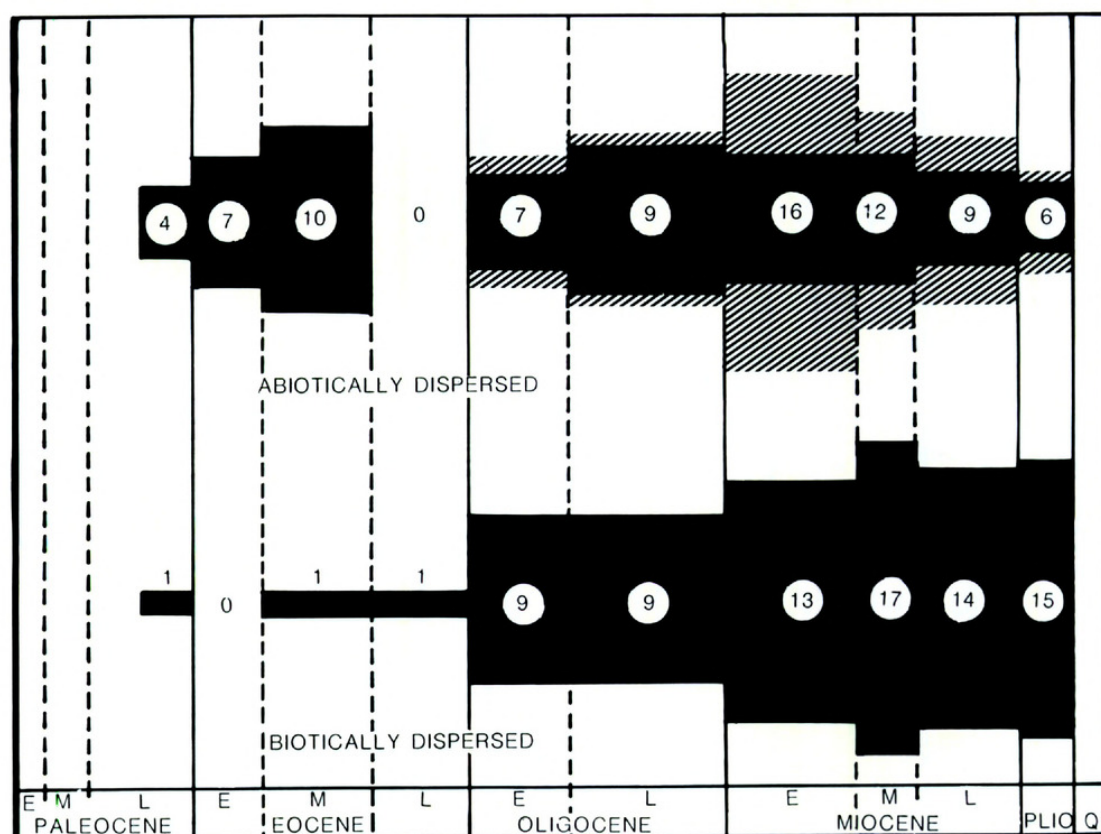
FIGURE 9. Specific diversity of abiotically-dispersed and biotically-dispersed Juglandaceae in the Tertiary. Data largely from Manchester (1981a); additional data from sources cited in Figure 6. Diagonally-lined area in upper spindle demonstrates the proportionately large contribution of *Pterocarya* to the diversity of abiotically-dispersed Juglandaceae in the later Tertiary. Numbers in each spindle indicate numbers of species present in each Epoch subdivision. Time convention as in Figure 1.

time within families. The fossil examples will be considered first and in order of increasing clarity.

Ulmaceae. The Ulmaceae is divided into the Ulmoideae (largely abiotically dispersed) and the Celtidoideae (largely biotically dispersed). Fruiting evidence of both subfamilies is recorded from the middle Paleocene (Fig. 3). Zavada and Crepet (1981) described flowers of Celtidoideae from the Middle Eocene of southeastern North America. In their discussion they noted that, in contrast to other Eocene fossil flowers of the "Amentifereae," which normally look modern at this time, these Celtidoid flowers were intermediate between insect-pollinated ancestors and the modern wind-pollinated flowers of the group. This conveys the impression that the Celtidoideae were still evolving in the mid-Eocene, and the hypothesis could be entertained that modern fruit and dispersal characters were also evolving in the group. However, such an interpretation ignores mosaic evolution and the likelihood that the evolutionary status of the flowers might have little to do with that of the fruits. Further, this interpretation presumes that the ulmoid flowers of the time were "modern," a conclusion for which no evidence exists. It is worth noting (Fig. 3) that, while two samaroid and two drupaceous genera are present in the Eocene, animal-dispersed forms have come to dominate the family by greater than a 2:1 margin. I suspect the Ulmaceae of having abiotic dispersal as the plesiomorphic state, but the actual evidence is very weak.

Fagaceae. Fagaceae are currently almost entirely animal dispersed. The Tertiary fossil record involves seven extant and two extinct genera. Of these, the extinct *Fagopsis* (Manchester & Crane, 1983) is both the earliest (Early Eocene through Late Oligocene) and is the only genus adapted to abiotic dispersal. The morphology of *Fagopsis* agrees with the cupules of other members of the family and argues for the derivation of structures for both biotic and abiotic dispersal from a common "cupule" morphology.

Late Cretaceous flowers from Massachusetts (Tiffney & Friis, unpubl. data) are similar to flow-

ers of extant Fagaceae, particularly those of *Lithocarpus.* The associated fruits are tiny, very numerous, and lack a cupule. Their great numbers and small size agree with Fey and Endress's (1983: 451) prediction that the origin of the cupule involved the reduction of the "highly branched system of modified (compact, sterile) ultimate parts of the inflorescential cyme." Such a reduction could also be linked to an increase in size of the remaining fruits, leading to the evolution of a single, large fruit. The tiny size and great numbers of these fruits argue for their abiotic dispersal.

The abiotic dispersal of the putative Cretaceous fagaceous fruits, together with the abiotic dispersal of the first clear fruit of the family to appear in the record, *Fagopsis,* suggests that the Fagaceae might be primitively abiotically dispersed. The rapid appearance of biotically-dispersed members of the family in the Tertiary could be seen as an adaptive response to the coeval radiations of mammals and birds.

Juglandaceae. Manchester (1981a; see also Manchester & Dilcher, 1982 and Wing & Hickey, 1984) has provided a detailed review of the history of the family with emphasis on its fruits. At the species level, abiotically-dispersed fruits dominated the early Tertiary record of the family; biotically-dispersed fruits diversified rapidly in the mid-Tertiary and dominate the family in the present day (Fig. 9). As found in the Fagaceae, this pattern is supported by Friis's (1983) data on three genera of fruits (*Manningia, Antiquocarya,* and *Caryanthus*) allied with the Juglandaceae in the Campanian. The mature fruits of all three are tiny and show no signs of fleshy parts leading one to assume abiotic dispersal.

This evidence suggests that the Juglandaceae (or the family and its immediate ancestors) were abiotically dispersed in the Late Cretaceous and earliest Tertiary. With the appearance of biotic dispersal agents, the family experimented with mechanisms of both biotic and abiotic dispersal. Presumably selection acted for larger endosperm reserves and therefore seed size (Tiffney, 1984) in the early Tertiary. This led to the simultaneous evolution of large-nutted, biotically-dispersed, fruits (*Juglans*) and the evolution of larger abiotically-dispersed fruits borne on increasingly larger winged structures (e.g., *Cyclocarya, Englehardtia*). The forms with animal-dispersed fruits ultimately dominated the family. Of the wind-dispersed forms, only *Pterocarya* was successful in the later Tertiary, perhaps because of its small

fruit and wing size; in the only reference to its site ecology, Wang (1961: 91) remarked that *Pterocarya stenoptera* C. DC. occurs "in small patches of pure communities in forest openings" implying that it is an early to mid-successional tree. This ecology is in keeping with the presumed early successional status (Tiffney, 1984) of the Late Cretaceous and Early Tertiary abiotically-dispersed members of the family.

Moraceae, Cecropiaceae, Urticaceae. Turning from the fossil record, there is evidence from the morphology of the Moraceae, Cecropiaceae, and to a degree, Urticaceae, that suggests these families underwent a transition from dominant abiotic to dominant biotic dispersal in their history. The Cecropiaceae are entirely animal dispersed today. In the extant Moraceae, 78% of the genera and 86% of the species are animal dispersed. The Urticaceae are mixed, with 47.6% of the genera and 29.3% of the species biotically dispersed. The common fruit morphology in all three families is an achene, or if the fruit wall is fleshy, a drupe. However, drupes occur in only 11% of the genera and 3% of the species in the Moraceae, only portions of one genus (*Coussapoa* Aubl.) of 50 species in the Cecropiaceae (20.7% of total number of species in the family), and only 4.3% of the genera and 1.3% of the species in the Urticaceae. Animal dispersal based on adherent fruits (sticky, hairy, or hooked) accounts for no more than 6% of the genera and 0.3% of the species of Moraceae and 13% of the genera and 12.8% of the species of Urticaceae. In all three families, the dominant structure associated with attracting animal dispersal agents involves either fleshy, accrescent calyx parts or an inflated, fleshy, receptacle. Both structures form succulent and attractively-colored berry mimics, but without the participation of the fruit wall; the fruit remains an achene buried in the externally-derived flesh. Many reports attest to the success of these "pseudo-drupes" in attracting birds or mammals [e.g., *Cudrania* Trécul, *Artocarpus* Forst., *Sloetia* Teij. & Binn. (*Streblus* Lour., see Ridley, 1930)]. Such "fruits" made of fleshy floral parts account for 67% of the genera and 82.8% of the species of Moraceae, 87.5% of the genera and 79.3% of the species of Cecropiaceae, and 30.3% of the genera and 15.2% of the species of Urticaceae. In some cases the floral parts aid in biotic dispersal by forming hairs or spines that stick to dispersal agents [e.g., *Rousselia* Gaudich. and *Soleirolia* Gaudich. (Urticaceae)]. Abiotic dispersal in all three families in-

volves both structures associated only with the achene and structures associated with the floral parts. In some genera [e.g., *Metatrophis* F. Brown (Moraceae), *Hemistylus* Benth. (Urticaceae)] the floral parts form wings, whereas in others [e.g., species of *Streblus* Lour., *Dorstenia* L. (Moraceae), *Pilea* Lindl., *Procris* Comm. ex Juss. (Urticaceae)] the calyx exerts pressure on the mature achenes and forces the fruits out of their floral envelope with great force (Ridley, 1930). Ballistic dispersal occurs in roughly 2% of the genera and 13% of the species of Moraceae, none of the Cecropiaceae, and 19.5% of the genera and perhaps as much as 58% of the species of Urticaceae.

The plesiomorphic status of the achene in this group is suggested but not proven by its wide distribution in all three families. It is also suggested by the fossil record, because the oldest fruiting remains of this group of families are achenes from the Late Cretaceous (Knobloch, 1971; Knobloch & Mai, 1984).

If abiotic mechanisms of dispersal dominated in the Cretaceous, and if the Urticaceae extend back to the Late Cretaceous, then it is possible that the dry and ballistically-dispersed achenes of the present day reflect the ancestral dispersal mechanisms of the Urticaceae, and by inference, the Moraceae and Cecropiaceae. If so, this implies that these families met the selective pressures of the evolving mammals and birds of the early Tertiary in two ways. The first was the evolution (once, or repeatedly) of fleshy exocarps to form drupes. To judge from the present day, this solution was not widespread. The second response was to build upon the specialization of the perianth, presumably already evolved for abiotic ballistic dispersal. Again, this potentially could have evolved repeatedly in several lineages. The accrescent floral parts could become fleshy, mimicking a berry without a topological re-arrangement of mature flower and fruit, or the developmental switch from a hard exocarp to a fleshy one underlain by a hard meso- or endocarp. This explanation is consistent with the important role that flower parts play in abiotic dispersal in the extant Urticaceae and to a lesser degree, Moraceae. It is also consistent with the perianth and receptacle-derived pseudo-berries that seem to form an important adaptive solution common to all three families. Tangentially, the early fossil record and the dominant abiotic dispersal mode of the Urticaceae suggests that they retain the greatest amount of plesiomorphic fruiting characters among the Cecropiaceae,

Moraceae, and Urticaceae. This could be related to their herbaceous growth habit. In either case, the ecological nature of the Urticaceae is consistent with the proposed abiotic dispersal ecology of the Cretaceous angiosperms (Tiffney, 1984).

SUMMARY

The fossil record of the Juglandaceae and its immediate predecessors strongly suggests a transition from abiotic to biotic dispersal within the family. The fossil evidence for the Fagaceae is less strong, but also suggestive of such a transition. Evidence for a similar transition in the Ulmaceae is inferential, but again suggestive. The dominance of perianth-derived pseudo-fruits in the Moraceae and Cecropiaceae and their presence in the Urticaceae, the commonality of the achene morphology to all three families, and the mechanisms of abiotic achene dispersal in the Urticaceae, may be hypothesized to reflect an early Tertiary transition from abiotic to biotic dispersal in the Moraceae and Cecropiaceae, and the retention of more plesiomorphic characters in the Urticaceae.

EVOLUTIONARY CONCLUSIONS

RELATIONSHIP OF DIVERSITY AND DISPERSAL MECHANISMS

The distribution of generic and specific diversities in the Hamamelidae presents an interesting pattern (Fig. 10). Sixteen families have three genera or less, and 14 have only one genus. Only three of these families have more than ten species (Daphniphyllaceae—35 spp., Casuarinaceae—50 spp., Myricaceae—50 spp.). Four families have an intermediate diversity; the Juglandaceae with 9/60 (genera/species), the Hamamelidaceae with 28/100 plus, the Betulaceae with 6/120, and the Ulmaceae with 18/150. Four families have high diversities: Cecropiaceae (8/275), Fagaceae (8/800), Urticaceae (46/1,255), and Moraceae (51/1,313).

It is commonly assumed that insect pollination is a primary cause of the present diversity of angiosperms. However, biotic dispersal of fruits and seeds offers a similar potential for animal-mediated diversification. The Hamamelidae provide a natural experiment to demonstrate the effect of biotic dispersal on diversity. With rare exceptions, the included families are dominated by anemophily (the Hamamelidaceae is primarily insect pollinated, and a few species in the
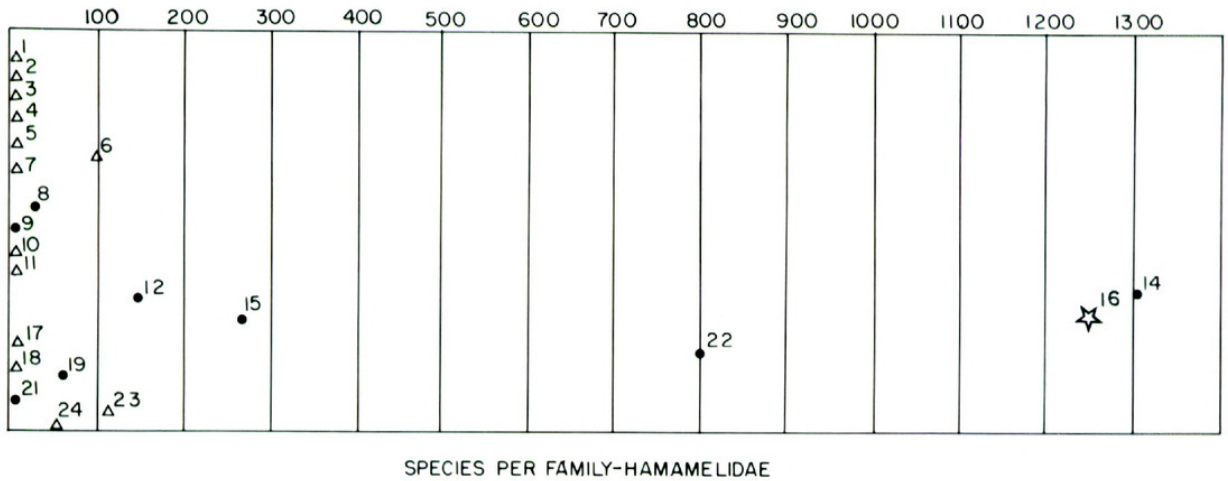
SPECIES PER FAMILY-HAMAMELIDAE

FIGURE 10. Plot of number of species per family for families in the Hamamelidae sensu Cronquist (1981). Points for Cannabaceae and Myricaceae omitted in light of absence of clear-cut dominant mode of dispersal. Horizontal axis, number of species; Vertical axis, valueless; Open triangles, families dominated by abiotic dispersal; Closed circles, families dominated by biotic dispersal; Open star, Urticaceae. Family identity indicated by the number by each symbol; the numbers corresponding to the order of families in Table 1.

Moraceae, Urticaceae, and Cecropiaceae are entomophilous, but these are unusual; similarly, the Fagaceae includes a few species that are secondarily entomophilous). In effect, the variable of insect pollination is controlled in the group. The only other variable that might confuse the proposed comparison is that of habit, however all the hamamelid families are dominantly (if not entirely) woody, with the exception of the Urticaceae, which are dominantly herbaceous.

Of the four families with substantially more than 150 species, only Urticaceae is not dominated by biotic dispersal. This anomaly may be explained largely by the herbaceous habit and shorter life cycle of most members of the latter family. Of the intermediate-sized families, Ulmaceae are dominated by biotic dispersal, Juglandaceae are dominated 2:1 by biotic dispersal, and Betulaceae possess both dispersal modes in unclear proportions. The Hamamelidaceae are abiotically dispersed, but their diversity could be explained by the dominant entomophily of the family. The small-sized families (50 species or less) are dominated (ten to four) by abiotic dispersal. A regression of species number per family against dispersal type (excluding data from the "generalized" Cannabaceae and Myricaceae) yields $r = 0.225$, below the 80% confidence limit. Elimination of the Urticaceae from the data set yields $r = 0.423$, which falls in the 90–95% confidence limit. Elimination of the Hamamelidaceae from consideration accentuates this effect. This pattern suggests the potential stimulating effect of biotic dispersal on the diversification of the angiosperms. The great diversity of the modern flora may be in large part a function of plant-animal interactions involving biotic diaspore dispersal, as well as the more frequently cited coevolution of angiosperms with pollinators and herbivores.

DISPERSAL PLASTICITY

Several examples demonstrate that dispersal mode changes within a family over time. Dispersal modes appear stable within genera, but this is an artifact: one would not identify an isolated fossil fruit as a modern genus unless it had the morphology of that genus. The demonstration of this plasticity is important on three counts. First, the appearance of animal-dispersed fruits within five to 15 million years after the radiation of mammals and birds in the early Tertiary is a measure of the reality of the concept of "coevolution" in a loose sense (cf. Herrera, 1985) and its significance in angiosperm evolution. Second, the response of fruit and seed morphology to the appearance of new dispersal agents further supports the importance of mosaicism in angiosperm evolution. For example, pollen data (Muller, 1981) suggest an earlier time of first appearance for many families than does that for fruits and seeds (Tiffney, unpubl. data). This suggests the separation of selective effects of pollinators and fruit/seed dispersers. Third, the flexibility of dispersal mechanisms over time within a family emphasizes the need to seek important phylogenetic characters of fruits and seeds in the

details of cell structure, cell layer sequence, etc., rather than simply in gross morphology.

EVALUATION OF HYPOTHESES

Two assumptions were made at the outset of this paper: (1) that the Hamamelidae originated and achieved their zenith in the Cretaceous, and (2) that Cretaceous angiosperms were largely abiotically dispersed and that biotic dispersal became important only in the early Tertiary. It is not possible to evaluate the first assumption from the fossil fruit and seed record, although fruiting material of some families (Platanaceae, Juglandaceae, possibly Urticaceae, and Fagaceae) is known from the Cretaceous. The second assumption (discussed by Tiffney, 1984) is supported by the apparent primitive status of abiotic dispersal demonstrated here for the Juglandaceae and possibly Fagaceae, and inferred for the Ulmaceae and possibly Moraceae, Cecropiaceae, and Urticaceae.

Given these assumptions, I predicted that (1) the majority of families in the Hamamelidae should have abiotic dispersal syndromes, and (2) that dispersal mode might provide an additional trait on which to assess the phylogenetic affinities of families whose alliance with the Hamamelidae has been questioned on other grounds.

The majority of families associated with the Hamamelidae in the scheme of Cronquist (1981) are abiotically dispersed (Table 1; 13 abiotic, seven biotic, and four either with roughly equal proportions of biotic and abiotic, or with generalized morphology and dispersal mechanism). However, evidence from the fossil record suggests that the Juglandaceae and perhaps Fagaceae underwent a transition from a dominantly abiotic mode of dispersal to a biotic mode in the early Tertiary; more circumstantial evidence suggests that the same might be true of the Ulmaceae and the Urticaceae and associated Moraceae and Cecropiaceae.

If the dominant mode of dispersal within a family can change over time, then the present dispersal characteristics are not an accurate guide of the past. The primitive dispersal state, while inferable from neontological evidence, can be demonstrated only through the fossil record. Thus, only in the case of the Juglandaceae, and perhaps of the Fagaceae, can we state that the primitive mode of dispersal was abiotic and that the dispersal mode does not contest the affinities of the family with the Hamamelidae. A similar transition from abiotic to biotic dispersal is suggested for the Ulmaceae by the fossil record, and for the Moraceae, Urticaceae, and Cecropiaceae by circumstantial morphological evidence; based on dispersal, the affinities of these families with the Hamamelidae cannot be evaluated. No fossil record exists for the Daphniphyllaceae, Didymelaceae, or Balanopaceae, thus there is no way to evaluate whether the biotic dispersal mechanisms of these taxa are primitive or derived.

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