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FOSSIL *CORYLOPSIS* AND *FOTHERGILLA* LEAVES (HAMAMELIDACEAE) FROM THE LOWER EOCENE FLORA OF REPUBLIC, WASHINGTON, U.S.A., AND THEIR EVOLUTIONARY AND BIOGEOGRAPHIC SIGNIFICANCE

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Corylopsis reedae Radtke, Pigg et Wehr sp. nov. and *Fothergilla malloryi* Radtke, Pigg et Wehr sp. nov. (Hamamelidaceae) are described from the lower Eocene (49–50 million years ago) Republic flora of northeastern Washington State. *Corylopsis reedae* is the first unequivocal fossil leaf report of *Corylopsis* Siebold & Zucc. (cv. Winter Hazel). The species is based on a single specimen that is 1.9 cm wide, preserved for 3.4 cm in length and estimated to be ca. 4 cm long, with an asymmetrical base and teeth that are concave apical, straight basal, with simple apices. The fossil leaf is remarkably similar to extant *Corylopsis*, with prominent compound agrophic veins; strong, straight secondaries; and closely spaced, ladder-rung-like, opposite to alternate percurrent tertiaries at right angles to the secondaries. Today this genus occurs only in Asia, but the fossil record, primarily of seeds, indicates it was widely distributed in North America and Europe during the Tertiary. *Fothergilla malloryi* documents conclusively the presence of this genus in the lower Eocene of North America for the first time. This leaf is 4.4 cm long × 3.5 cm wide and slightly lobate, with low, widely spaced teeth on the margin, an asymmetric apex, and a cordate base. This occurrence represents the oldest record for the genus, which is also known in the Oligocene of North America and several Neogene Asian localities. Today, *Fothergilla* (cv. Witch Alder) is native to southeastern North America. The occurrence at Republic of these two hamamelid plants underscores the diversity of the northwestern "Okanogan Highlands" flora of British Columbia, Canada, and Washington State, and demonstrates the Early Eocene presence of two disjunct hamamelid genera. These occurrences provide new data for better understanding the evolution and biogeography of the family.

Keywords: biogeography, *Corylopsis*, Hamamelidaceae, fossil leaves, *Fothergilla*, Eocene.

Introduction

Plants traditionally recognized in the family Hamamelidaceae comprise ca. 31 genera and 144 species of trees and shrubs that today are distributed primarily in tropical and subtropical mountainous regions (Endress 1989*a*, 1989*b*; Zhang and Lu 1995; Li and Bogle 2001; Judd et al. 2002). This family includes ornamental trees known for their showy floral structures, two of which, *Corylopsis* Siebold & Zucc. (cv. Winter Hazel), a genus of ca. 7–30 species, and *Fothergilla* L. (cv. Witch Alder), with two species, are widely planted as cultivars in warm temperate regions (Bir 1992; Dirr 1992; Dunnett 1992). The present distributions of *Corylopsis*, an Asian genus today, and *Fothergilla*, native to southeastern North America, are greatly restricted from earlier, more widespread occurrences in the Tertiary.

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The fossil record of *Corylopsis* is based primarily on seeds with a distinctive hilar scar that distinguishes them from other hamamelidaceous genera (Grote 1989; Manchester 1999). Fossil *Corylopsis* seeds are known from the lower Tertiary of southern England (Chandler 1961), the Eocene Claiborne Formation of southeastern North America (Grote 1989), fruits and seeds from the upper Eocene of Germany (Mai and Walther 1985), and fruits from the Miocene of Denmark (Friis 1985). Later Neogene occurrences in Europe include seed and fruit fossils in Germany and Poland during the Pliocene (Grote 1989), in the Netherlands during the middle Pliocene (Reid and Reid 1915), and in Poland during the lower Pleistocene (Tralau 1963). Fossil leaves attributed to *Corylopsis* have been described from the Eocene of Alaska (Wolfe 1972, 1977), and others referred to the genus *Corylopsiphyllum* Koch are known from the Paleogene of Greenland and Japan (Mathiesen 1932; Koch 1963). Whereas these specimens show some features in common with leaves of extant *Corylopsis*, they cannot be unequivocally identified. Pollen attributed to the genus has been reported from the Tertiary of Scotland (Simpson 1936) and the Eocene of southern Russia (Aristova 1973). The corresponding fossil wood genus *Corylopsites* Mathiesen is known from the Paleogene of Greenland (Mathiesen 1932). Floral mesofossil remains of Santonian age from eastern North America and

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leaves of the Maastrichtian Medicine Formation of Montana share some similarities with *Corylopsis*, but their relationship to the modern genus is unclear (Crabtree 1987; Magallón et al. 2001).

Fothergilla has a fossil record that includes leaves from the Oligocene Bridge Creek flora of Oregon and of Kazakhstan (Meyer and Manchester 1997) and the Miocene of Shantung, China (Hu and Chaney 1940), and Japan (Suzuki 1961). Pollen has been reported from the Eocene of Siberia (Kulkova 1973), but this record has not been substantiated (Muller 1981). As with *Corylopsis*, Maastrichtian-aged leaves from Montana resembling *Fothergilla* are known, but affiliations to the extant genus are not understood (Crabtree 1987).

In this study, we describe *Corylopsis reedae* Radtke, Pigg et Wehr sp. nov. and *Fothergilla malloryi* Radtke, Pigg et Wehr sp. nov., lower Eocene fossil leaves from the high-diversity Republic flora of northeastern Washington State. These fossils have the distinctive features found in modern leaves of *Corylopsis* and *Fothergilla*, including characteristic details of leaf morphology, venation, and marginal teeth. These discoveries firmly establish the Early Eocene presence in northwestern North America of these two contrasting disjunct hamamelid genera, one native to Asia and the other to southeastern North America today.

Material and Methods

We examined fossils from the Republic flora of northeastern Washington State, a site within the Early Eocene Okanogan Highlands. Stratigraphically, these fossils occur within the Klondike Mountain Formation, which was deposited between 50 and 49 Ma. Previous studies have generally recognized this locality as middle Eocene, but recent changes by the International Commission on Stratigraphy (Working Group on Stratigraphic Information System [SIS]; http://www.stratigraphy.org) places the Early-Middle (Ypresian-Lutetian) boundary at 48.6 ± 0.2 Ma (B. Archibald, Harvard University, personal communication). Based on ^{40}Ar-^{39}Ar decay, the date has recently been set at 49.4 ± 0.5 Ma (Wolfe et al. 2003). The Republic flora is highly diverse and has yielded more than 350 species of fossilized plants (Wehr and Hopkins 1994). The flora found here represents a broad array of taxa indicative of microthermal and equable conditions at higher and lower elevation sites, respectively (Johnson 1996; DeVore et al. 2005).

Fossil leaf compressions were photographed on Ektachrome 160 ASA tungsten 35 mm film, and slides were scanned with a Nikon 2000 slide scanner. Some images were obtained by directly scanning fossil and extant leaves on a UMAX Astra 1200S flatbed scanner. Digital images were burned onto CDs with Adaptec Easyscan software and processed with Adobe Photoshop 6. Leaves of extant *Corylopsis*, *Fothergilla*, and several other genera of Hamamelidaceae were prepared using a mixture of chloral hydrate, clove oil, lactic acid, phenol, and xylene (2 : 2 : 2 : 2 : 1), with the leaves allowed to remain in the solution until cleared (Ruzin 1999, pp. 128–129). After clearing, they were rinsed, bleached in a 1 : 1 mixture of hydrogen peroxide and glacial acetic acid, heated until they turned white, and then rinsed and stored in

ethanol. Terminology follows the *Manual of Leaf Architecture* (Leaf Architecture Working Group 1999).

Systematics and Descriptions

Family—Hamamelidaceae

*Genus—*Corylopsis *Siebold & Zucc.*

*Type species—*Corylopsis pauciflora *Siebold & Zucc. Fl. Jap. 1:48. 1835*

*Species–*Corylopsis reedae *Radtke, Pigg et Wehr sp. nov. (Fig. 1A, 1D; Fig. 2B, 2E, 2F, 2H, 2I)*

Synonomy. *Corylopsis* Wehr and Hopkins 1994, plate 1, figure 7.

Diagnosis. Lamina of incomplete length but estimated to be ca. 4 cm long, 1.9 cm wide, elliptical, slightly asymmetrical, unlobed, and with a length-width (L/W) ratio of ca. 2 : 1; base convex, asymmetric, obtuse (102°); apex estimated to be convex, apex angle estimated to being slightly acute (ca. 88°); margin serrate; secondary veins pinnate, craspedodromous, strongly delimited, straight; prominent sets of compound agrophic veins produced basally; straight, closely spaced, ladder-rung-like, opposite to alternate percurrent tertiaries produced at right angles to the secondaries; quaternary veins alternate/percurrent; quinternary veins polygonal reticulate, aeroles regular, well developed; freely ending veinlets; marginal vein-producing loops within leaf margin; teeth concave apical, straight basal, with simple apices.

Holotype. UWBM 71085 (University of Washington, Burke Museum of Natural History and Culture; fig. 1*A*, 1*D*; fig. 2*B*, 2*E*, 2*F*, 2*H*, 2*I*).
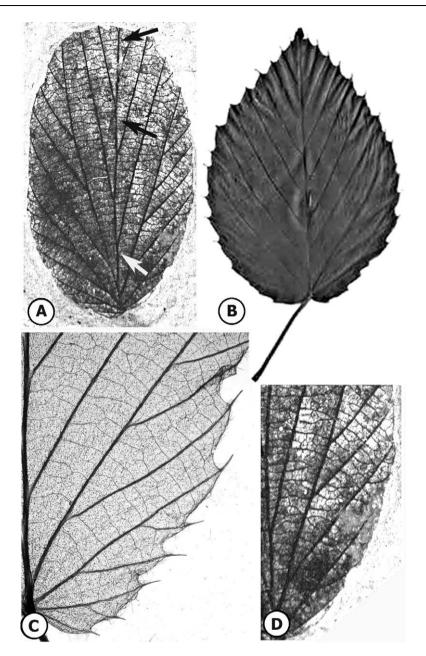
Type locality. Corner Lot (UWBM Loc. A0307), Republic, Ferry County, Washington.

Age and stratigraphy. Lower Eocene Klondike Mountain Formation, 49.4 ± 0.5 Ma, based on ^{40}Ar-^{39}Ar decay (Wolfe et al. 2003).

Etymology. The species name, "reedae," honors Katherine ("Kitty") M. Reed, for her numerous contributions to Northwestern Tertiary paleontology and stratigraphy.

Description. *Corylopsis reedae* Radtke, Pigg et Wehr sp. nov., based on a single specimen from the Corner Lot locality, Republic, Washington, is similar in all available details to modern *Corylopsis* (figs. 1, 2). The fragmentary leaf is 3.4 cm long, missing its apical tip, 1.9 cm wide, and slightly asymmetrical (fig. 1*A*). Based on its general morphology and in comparison with similar extant leaves, we estimate its length to be ca. 4 cm, with an L/W ratio of ca. 2 : 1. The lamina is elliptic, with evidence of a serrate margin, and has a convex, asymmetrical base. The midrib is fairly straight, bending slightly near the apex. Secondary venation is pinnate craspedodromous, with alternately produced, strongly developed, straight veins that are evenly spaced, produced 7–8 mm apart and paralleling one another at a distance of 2 mm (fig. 1*A*, 1*D*). The basalmost secondaries diverge at an angle of 18° with the midrib, while more apical secondaries have a more acute angle of 13°–14° with the midrib (fig. 1*A*).

Conspicuous features of this leaf type are the strongly delimited, straight secondaries, the closely spaced, crowded tertiaries, and the compound agrophic veins that originate

Fig. 1 Overview of leaves. *A, D,* Fossil *Corylopsis reedae* sp. nov., UWBM 71085. *B, C,* Extant *Corylopsis spicata. A,* Overview of leaf. Arrows indicate position of midvein; ×2.2. *B,* Extant *C. spicata* leaf, for comparison; ×3.8. *C, D,* Lateral side of extant (×3) and fossil (×3.7) leaves, respectively, showing prominent agrophic veins and ladder-like tertiaries.
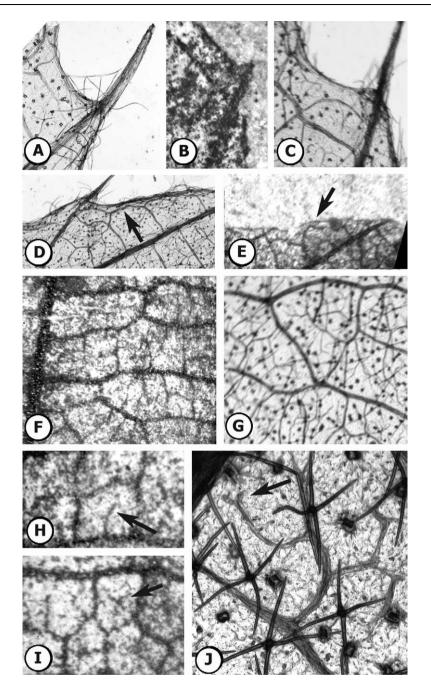
basally (fig. 1*A*, 1*D*). Tertiaries are straight and ladder-rung-like, opposite to alternate percurrent, and produced at right angles to the secondaries (fig. 1*D*; fig. 2*F*). Quaternaries are alternate/percurrent, and fifth-order veins are regular polygonal reticulate (fig. 2*F,* 2*H,* 2*I*). A marginal vein is formed by a series of loops right below the margin of the leaf (fig. 2*E*). Freely ending veinlets are either unbranched (fig. 2*H*) or forked (fig. 2*I*). The leaf margin, where preserved, shows the base of partially preserved teeth that are concave apical and straight basal, with a single vein extending into the tooth (fig. 2*B*). Teeth have been broken off, so their original length

is uncertain. Glands are not present, but their absence may be preservational.

Genus—Fothergilla *L.*

Type species—Fothergilla gardenii *L.*

Species—Fothergilla malloryi *Radtke, Pigg et Wehr sp. nov.* (Fig. 3A, 3C, 3F; Fig. 4A, 4D)

Diagnosis. Leaf simple, ovate, 4.4 cm long × 3.1 cm wide centrally, widening to 3.5 cm basally; L/W ratio 1.4 : 1; base rounded/cordate; slightly asymmetric; secondary venation

Fig. 2 Detail of leaf venation. *A, C, D, G, J,* Extant *Corylopsis spicata*; *B, E, F, H, I, Corylopsis reedae* sp. nov., UWBM 71085. *A, C,* Detail of extant *C. spicata* showing teeth at leaf margin (×7). *B,* Fossil leaf margin showing partially preserved tooth and venation (×7). *D, E,* Extant and fossil leaf margins, respectively, showing marginal looped vein (arrows) (×5). *F, G,* Fossil (×18) and extant (×16) leaves, respectively, showing detail of venation. *H, I,* Fossil leaves showing simple and forked freely ending veinlets (arrows) (×25). *J,* Extant leaf showing freely ending veinlets (arrow), trichomes, and trichome bases (×10).

pinnate, craspedodromous; festooned brochidodromy; secondaries diverge at angle of 53°, tertiaries mixed opposite-alternate, quaternaries alternate/percurrent; leaf margin crenate with large rounded teeth, convex apical, convex basal, broad at base.

Holotype. UWBM 56625 (fig. 3*A*, 3*C*, 3*F*; fig. 4*A*, 4*D*).

Type locality. Boot Hill (UWBM Loc. B4131), Republic, Ferry County, Washington.

Age and stratigraphy. Early Eocene Klondike Mountain Formation, 49.4 ± 0.5 Ma, based on ^{40}Ar-^{39}Ar decay (Wolfe et al. 2003).

Etymology. The species is named in honor of Dr. V. Standish Mallory, for his numerous contributions to the Tertiary paleontology of Washington State.

Description. Fothergilla malloryi Radtke, Pigg et Wehr sp. nov. is based on a single specimen from the Boot Hill

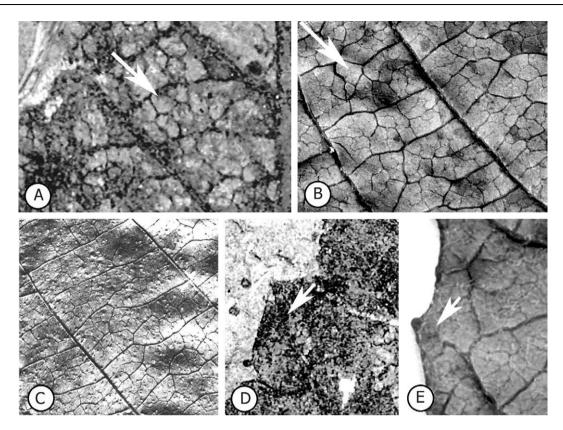**Fig. 3** Overview and detail of leaves. *A, C, F, Fothergilla malloryi* sp. nov. *B, D, E,* Extant *Fothergilla gardenii,* for comparison. *A,* Overview of fossil leaf, UWBM 56625 (×1.2). *B,* Extant *F. gardenii* (×1.1). *C, D,* Detail of leaf apex and margin of *F. malloryi* (×2.3) and *F. gardenii* (×2), respectively. *E, F,* Detail of leaf base and petiole of *F. gardenii* (×2.5) and *F. malloryi* (×2.1), respectively.

locality, Republic, Washington, that shares morphological features with extant *Fothergilla* (figs. 3, 4). The leaf has an ovate lamina that is 4.4 cm long × 3.1 cm wide centrally, widening basally to a maximum of 3.5 cm across, with a L/W ratio of ca. 1.4 : 1. The leaf base is rounded/cordate and slightly asymmetric, with an obtuse angle of ca. 125° (fig. 3*A*, 3*F*). The leaf apex is partially preserved, obtuse, and asymmetric (fig. 3*A*, 3*C*). The petiole is at least 7 mm long and appears broken at the base, with a fragment 4.5 mm long below the break that may be part of the structure, suggesting that the petiole was at least 15 mm long × 1 mm across at its widest part (fig. 3*A*, 3*F*). It extends into a midrib that is ca. 0.7 mm thick.

Venation is pinnate craspedodromous, with secondaries that diverge at a fairly broad angle of ca. 53°, curving slightly toward the apex (fig. 3*A*). Seven pairs of alternately produced secondaries extend from the midvein and end in festooned brochidodromy (fig. 3*A*, 3*F*; fig. 4*E*). Tertiaries are mixed opposite-alternate, quaternaries are alternate/percurrent, and fifth-order veins are regular polygonal reticulate (fig. 4*A*, 4*D*). The leaf margin is crenate, with large, rounded teeth that are widely spaced, with approximately two teeth per square centimeter (fig. 3*A*, 3*C*; fig. 4*D*). The teeth are simple, convex apical, convex basal, and very broad at their base. They are vascularized by a simple major vein, with obscure accessory veins, that extends into a small tip, which appears glandular (fig. 4*D*).

Fig. 4 Selected leaves of Hamamelidaceae, showing details of venation and margin. *A–D*, Higher-order venation, with arrows indicating similar point of reference. *A*, Fossil *Fothergilla malloryi* (×8). *B*, *Fothergilla gardenii* (×7). *C*, *Hamamelis virginiana* (×7). Note similarities in secondary, tertiary, and higher-order venation. Also note that *Hamamelis* has a similar pattern but much less pronounced venation. *D, E*, Detail of tooth and venation. Arrows are pointing to the single large vein that enters the tooth. *D*, *F. malloryi* (×15); *E*, *F. gardenii* (×10).

Discussion

Corylopsis *and* Fothergilla *Leaves from Republic*

The discovery of *Corylopsis reedae* sp. nov. and *Fothergilla malloryi* sp. nov. leaves from Republic documents the presence of these two distinctive hamamelid genera in the lower Eocene Okanogan Highlands floras of western North America. The fossil leaves have diagnostic features that are remarkably similar to those of leaves of their modern counterparts. However, because extant species are based primarily on floral structures not available in the fossils, the fossils cannot be assigned with confidence to extant species. They are, therefore, delimited as new species based on leaf morphological features.

Corylopsis. The taxonomy of extant *Corylopsis* is complex, with many species with restricted endemic distributions in China (Morley and Chao 1977; Li and Bogle 2001; Wu et al. 2003, pp. 18–42). Important leaf features of the genus *Corylopsis* present in *C. reedae* include elliptical laminar shape; asymmetric base; very well developed, compound agrophic (=pectinal of Spicer 1986) veins; strongly defined, straight secondaries that are evenly spaced centrally and become more crowded and more obtusely angled basally; and strong, crowded tertiary veins perpendicular to secondaries. Conspicuous spinose teeth that characterize some extant species are

not completely preserved in *C. reedae*, but details of the partly preserved teeth are consistent with those of extant forms.

Fossil leaves from the Eocene of Alaska and the Paleogene of Greenland have been referred to the genus *Corylopsis* and the similar taxon *Corylopsiphyllum*, respectively. *Corylopsis* sp. was described from the late Eocene Kushtaka Formation of Alaska on the basis of a single specimen (Wolfe 1972 [pl. 6, fig. 4], 1977 [p. 70, pl. 26, fig. 6]). From the illustration, the partially preserved leaf is measured to be ca. 2.3 cm long × 1.8 cm wide, lacks a complete base (described as "cordate"; Wolfe 1977), and also lacks an apex. It has a relatively straight midvein and has perhaps four pairs of lateral secondaries that are produced at ca. 40° with the midvein. Secondaries appear transitional between subopposite and truly alternate, follow a straight course basally, and curve slightly inward apically. At least three simple agrophic veins are produced at the base on one side of the lamina. The specimen provides little further detail, and the margin is difficult to delimit, although Wolfe (1977) describes it as having markedly sharp, "almost spinose" teeth.

Corylopsiphyllum groenlandicum Koch is the name given to five leaf specimens from the Paleogene of central Greenland (Koch 1963). These leaves are considerably larger than both *Corylopsis malloryi* (estimated to be ca. 4 cm long) and the small leaf described by Wolfe (1972, 1977; <3 cm long). The most completely preserved leaves of *Corylopsiphyllum*,

as measured from the figured specimens, are ca. 8 cm long × 4.7 cm wide, lacking their bases; the largest incomplete fragment is 10 cm long and 7.5 cm wide. Complete leaves are estimated to have been up to 15 cm long × 7.5 cm wide, probably with a ca. 1.7–2 : 1 L/W ratio. Secondaries are alternately produced (except for the basalmost opposite pair), pinnate, straight to slightly curved inward, and evenly spaced. Agrophic and possibly compound agrophic veins are formed. Higher-order venation is described as polygonal, and the margin is dentate, with conspicuous "thread point" teeth (Koch 1963). Koch (1963) compares these leaves to both *Corylus* and *Corylopsis*, particularly in features of the leaf margin, and concludes that they are more similar to the latter. The leaf base, described as "broadly cuneate," appears incompletely preserved. Although these leaves have many hamamelid features, their assignment to *Corylopsis* does not appear conclusive. Further study of additional specimens is probably needed to more clearly delimit the relationship of *Corylopsisiphyllum* to extant genera.

Fothergilla. *Fothergilla* leaves can vary in shape from elliptic to obovate and ovate to nearly orbiculate. They are typically characterized by an obtuse, oblique base and an acute to rounded apex. Venation includes pinnate secondaries with festooned brochidodromy and relatively few and simple agrophic veins. Leaf margins are entire to crenate to serrate (Ernst 1963; Weaver 1969; Meyer 1997). Extant *Fothergilla* is represented by two species of relatively uncommon scrambling shrubs, both endemic to southeastern North America today. Leaves of *Fothergilla gardenii* L. native to the Coastal Plain are relatively small (usually <2.5 cm long; Weaver 1969), somewhat coriaceous, with basally entire, apically toothed margins and slightly asymmetric leaf bases. In contrast, those of *Fothergilla major*, which occurs in higher-elevation piedmont and mountainous regions, are larger (>2.5 cm long), thinner, and typically more completely crenate to serrate margined and have more conspicuously oblique leaf bases (Weaver 1969; Meyer 1997).

Fossil leaves of *Fothergilla* all fall more closely within the size range and morphological descriptions of the extant Coastal Plain species *F. gardenii*, although there is a wide range of morphological variability among all fothergillas. Among previous reports of fossil leaves, *F. malloryi* is most similar to *Fothergilla viburnifolia* Hu & Chaney from the Middle Miocene Shantung flora of China (Hu and Chaney 1940). *Fothergilla malloryi* fits within the size range of *F. viburnifolia* and is somewhat smaller than the mean (4.4 vs. 5.1 cm in length); however, this leaf is ovate with an oblique cordate base and slightly asymmetric apex, while leaves of *F. viburnifolia* are rhomic obovate with a narrowly rounded leaf base and an apex that is often acuminate.

The Japanese Miocene species, *Fothergilla ryozenensis* Suzuki, is also quite similar but larger and more elongate. It has an acuminate rather than an obtuse apex and a truncate rather than a round/cordate base (Suzuki 1961). The Oligocene taxon *Fothergilla praeolata* Meyer & Manchester, from the Bridge Creek flora of Oregon, has characters that fall readily within the genus *Fothergilla*, but it differs from *F. malloryi* in overall shape, as well as having an acute to emarginate apex and an inflated petiole (Meyer and Manchester 1997). A leaf from the Eocene of King County, Washington, described as *Fothergilla durhamensis* Wolfe, is less convincing, as it has what appear to be more generalized characters found in several of the temperate hamamelid genera such as *Hamamelis* L. and *Parrotia* Mey. (Wolfe 1968, 1973; Klucking 1995).

Table 1

Megafossils of Hamamelidaceae

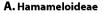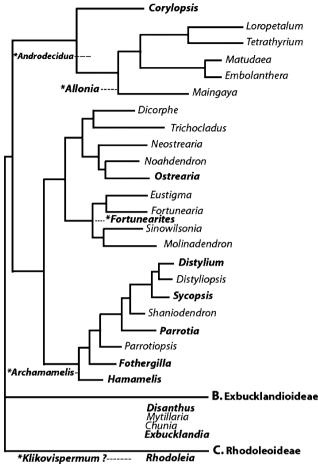| Taxon	Late Cretaceous		Paleogene		Neogene			
	TS	CM	P	EO	O	M	PL	R
Hamamelidaceae	N,[a] E,[a] A[a]	N,[a] E[a]						
Corylopsis	N[a]	N[a]		N,[b] E	E	E	E	A
Disanthus				A	A	E		A
Distylium				A, N	E	E		A, N
Exbucklandia					N	A, N		A
Fortunearia		N[a]		N[a]	E	A, E	E	A
Fothergilla		N[a]		N[b]	A, N	A, N		N
Hamamelis	E[a]	N[a]	N		A	A		A, N
Lorapetalum	N[a]							A
Matudaea					E	E		N
Parrotia					N	A, E	A, E	A
Rhodoleia		E[a]		E				A
Sinowilsonia		N[a]		N[a]				A
Sycopsis	N[a]							A

Note.   TS = Turonian-Santonian; CM = Campanian-Maastrichtian; P = Paleocene; EO = Eocene; O = Oligocene; M = Miocene; PL = Pliocene; R = Recent; N = North America; E = Europe; A = Asia; from Hu and Chaney (1940); Lakhampal (1958); Suzuki (1961); Tanai (1970); Gregor (1977); Knobloch and Mai (1986); Tiffney (1986); Crabtree (1987); Crane et al. (1990); Endress and Friis (1991); Crepet et al. (1992); Manchester (1994, 1999); Magallón-Puebla et al. (1996); Meyer and Manchester (1997); Herendeen et al. (1999); Magallón et al. (1999, 2001); Takahashi et al. (1999); Henry and Pigg (2001).

[a] Related extinct taxon.

[b] This study.

A. Hamameloideae

- *Corylopsis*
- *Androdecidua*
  - *Loropetalum*
  - *Tetrathyrium*
  - *Matudaea*
  - *Embolanthera*
  - *Allonia* — *Maingaya*
- *Dicorphe*
- *Trichocladus*
- *Neostrearia*
- *Noahdendron*
- *Ostrearia*
- *Eustigma*
- *Fortunearia*
- *Fortunearites*
- *Sinowilsonia*
- *Molinadendron*
- *Distylium*
- *Distyliopsis*
- *Sycopsis*
- *Shaniodendron*
- *Parrotia*
- *Parrotiopsis*
- *Fothergilla*
- *Hamamelis*
- *Archamamelis*

B. Exbucklandioideae
- *Disanthus*
- *Mytillaria*
- *Chunia*
- *Exbucklandia*

C. Rhodoleoideae
- *Klikovispermum ?* — *Rhodoleia*

Fig. 5 Relationships of Hamamelidaceae. Phylogenetic relationships of Hamamelidaceae depicted from topology of subfamily Hamamelidoideae (*A*) redrawn from Li and Bogle (2001). Subfamilies Exbucklandiodeae (*B*) and Rhodoleoideae (*C*) are included but not designated in any particular hypothesis of relationship. Genera in boldface have a fossil record (see table 1); those with an asterisk are extinct fossil genera that have been mapped onto the clades in their hypothesized phylogenetic positions. See table 1 for details.

Significance to the Evolutionary History of Hamamelidaceae

Corylopsis and *Fothergilla* leaves at Republic are among the earliest occurrences of extant genera in the family (table 1; fig. 5). Before the Eocene, the group is represented by several types of Late Cretaceous floral remains from assemblages in eastern North America, Europe, and Japan that show a mosaic of hamamelid features (Endress and Friis

1991; Crepet et al. 1992; Magallón et al. 1999, 2001; Herendeen et al. 1999; Takahashi et al. 1999). Leaves with presumed hamamelid affinities occur in a variety of Maastrichtian sites (Crabtree 1987). In the Paleocene of North America, a *Hamamelis*-like infructescence and associated seeds and pollen catkins are known (Crane et al. 1990; Henry and Pigg 2001). However, it is in the Eocene that the modern genera *Corylopsis*, *Fothergilla*, *Disanthus*, *Distylium*, and *Rhodoleia* first appear, along with *Fortunearites*, an extinct genus similar to *Fortunearia* and *Sinowilsonia* (fig. 5; Manchester 1994). *Exbucklandia*, *Parrotia*, and *Matudaea* make their first appearance in the Oligocene. All clades of Hamamelidaceae except the *Dicoryphe* clade thus have fossil representatives, supporting the suggestion that the *Dicoryphe* clade, an exclusively Gondwanan group, may have radiated quite recently (table 1; fig. 5).

Based on the fossil record, the most common biogeographic pattern within the Hamamelidaceae, including the one seen in *Corylopsis*, is that of a Late Cretaceous origin in North America, followed by dispersal into Europe and eventual migration to a present-day Asian distribution (table 1; fig 5). *Fothergilla*, in contrast, apparently had its earliest occurrence in North America at Republic and then demonstrated a "temporary" presence in Asia during the Neogene, but today it has an exclusively North American distribution (DeVore et al. 2005). In contrast to these two patterns, the other major temperate genus, *Hamamelis*, retains an Asian/North American disjunction today (Wen and Shi 1998).

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