HAMAWILSONIA BOGLEI GEN. ET SP. NOV. (HAMAMELIDACEAE) FROM THE LATE PALEOCENE ALMONT FLORA OF CENTRAL NORTH DAKOTA

John C. Benedict,* Kathleen B. Pigg,[1],* and Melanie L. DeVore†

*School of Life Sciences, Arizona State University, P.O. Box 874501, Tempe, Arizona 85287-4501, U.S.A.; and †Department of Biological and Environmental Sciences, CBX 081, Georgia College and State University, Milledgeville, Georgia 31062-0001, U.S.A.

Hamawilsonia boglei Benedict, Pigg & DeVore gen. et sp. nov. (Hamamelidaceae) is described from the Late Paleocene Almont flora of central North Dakota. The infructescence is an anatomically preserved spike with up to 20 sessile, robust, cuboidal to ovoid capsules borne on an elongate, thick axis up to 9.2 cm long × 0.5 cm wide. Individual fruits are 10–12 mm across and bilocular, with paired persistent, recurved styles borne on the distal carpel face. One locule is often larger than the other. Anatomically, the fruit wall is composed of a sclerified endocarp and a poorly preserved exocarp. Seeds are elliptical to slightly obovate with a sclerotic seed coat. *Hamawilsonia* is an extinct Late Paleocene genus with a combination of characters not seen in any extant hamamelid genus. *Hamawilsonia* is similar to the Asian endemic genus *Sinowilsonia* in its elongate spikelike infructescence, resembles the witch hazel *Hamamelis* in fruit and seed morphology, and has seed anatomy that combines features found in several extant genera. Affinities with *Sinowilsonia* are further supported by the co-occurrence of associated pollen catkins and in situ tricolpate pollen with a distinctive reticulate sculpturing. Like several other Almont taxa (*Amersinia*, *Beringiaphyllum*, *Davidia*, and *Palaeocarpinus*), *Hamawilsonia* is a genus with strong North American–Asian affinities.

Keywords: Almont, biogeography, explosive dehiscence, *Hamamelis*, Hamamelidaceae, Hamamelidoideae, Paleocene, *Sinowilsonia*.

The Hamamelidaceae are a family of 31 extant genera and 144 species of trees and shrubs, distributed mostly in the mountainous regions of the subtropics (Endress 1993; Judd et al. 2002). The family has traditionally been subdivided into four to six subfamilies (Harms 1930; Endress 1989*c*). Endress (1989*c*) proposed a taxonomic classification of Hamamelidaceae that recognized four subfamilies: Hamamelidoideae, Exbucklandoideae, Rhodoleiodeae, and Altingioideae. The largest of these, Hamamelidoideae, includes 22 genera, seven of which are north temperate in the Eastern and Western Hemispheres, with the remaining taxa occurring in the Paleotropics and Neotropics (fig. 1). Subfamily Exbucklandoideae includes the Asian genera *Exbucklandia* R.W. Br. and *Disanthus* Maxim. The Asian subfamily Rhodoleioideae Harms is monotypic, with the genus *Rhodoleia* Champ. The previously recognized subfamily Altingioideae (sometimes termed Liquidambaroideae; Ferguson 1989) is now established as the family Altingiaceae (APG 2003; Ickert-Bond et al. 2005, 2007). A detailed taxonomic history of the Hamamelidaceae has been summarized by Endress (1989*c*) and Li (1997).

Recent molecular work has markedly changed the way the Hamamelidaceae is viewed, from its previous status as a member of the traditional "Lower Hamamelidae" sensu Cronquist (Cronquist 1981; Endress 1989*a*, 1989*c*) to its current position within the Saxifragales (Judd et al. 2002; APG 2003). Li and Bogle (2001) presented a new classification of genera within the subfamily Hamamelidoideae that recognized six tribes. Their phylogenetic analyses, based on morphology and nuclear and chloroplast DNA sequence data, resulted in the recognition of three major clades. Li and Bogle's (2001) classification differs somewhat from that of Endress (1989*c*); however, the taxa that are not corresponding are ones that are not pertinent to the central discussion of this article. We will refer to the loropetalid, eustigmatid, and fothergillid clades below (fig. 1).

The Hamamelidaceae have a rich fossil record (Tiffney 1984; Radtke et al. 2005; Magallón 2007) extending from the Late Cretaceous to the present. Among the reproductive structures assigned to this family are flowers from the Late Cretaceous of Sweden (Endress and Friis 1991), eastern North America (Crepet et al. 1992; Magallón-Puebla et al. 1996; Herendeen et al. 1999; Magallón et al. 2001), and Japan (Takahashi et al. 1999). These mesofossil remains are all of extinct forms with a mosaic of floral features found in combinations not known in extant genera, and they represent two different clades (summarized by Radtke et al. 2005; evaluated by Magallón 2007).

Fruits and seeds of the middle Eocene *Fortunearites* Manchester, a taxon with similarities to *Fortunearia* Rehd. & Wils. and *Sinowilsonia* Hemsl., are known from the Clarno flora of Oregon along with an associated, unnamed pollen catkin (Manchester 1994). Isolated seeds attributed to *Corylopsis* Sieb. & Zucc. have been described from the middle Eocene of southeastern North America (Grote 1989), the Neogene of Europe (Tralau 1963; Mai and Walther 1985), and, most recently, the Miocene of China (Zhao et al. 2008). Hamamelid pollen (Muller 1981) and fossil woods (Wheeler and Manchester 2002) are summarized elsewhere, and hamamelid leaves are
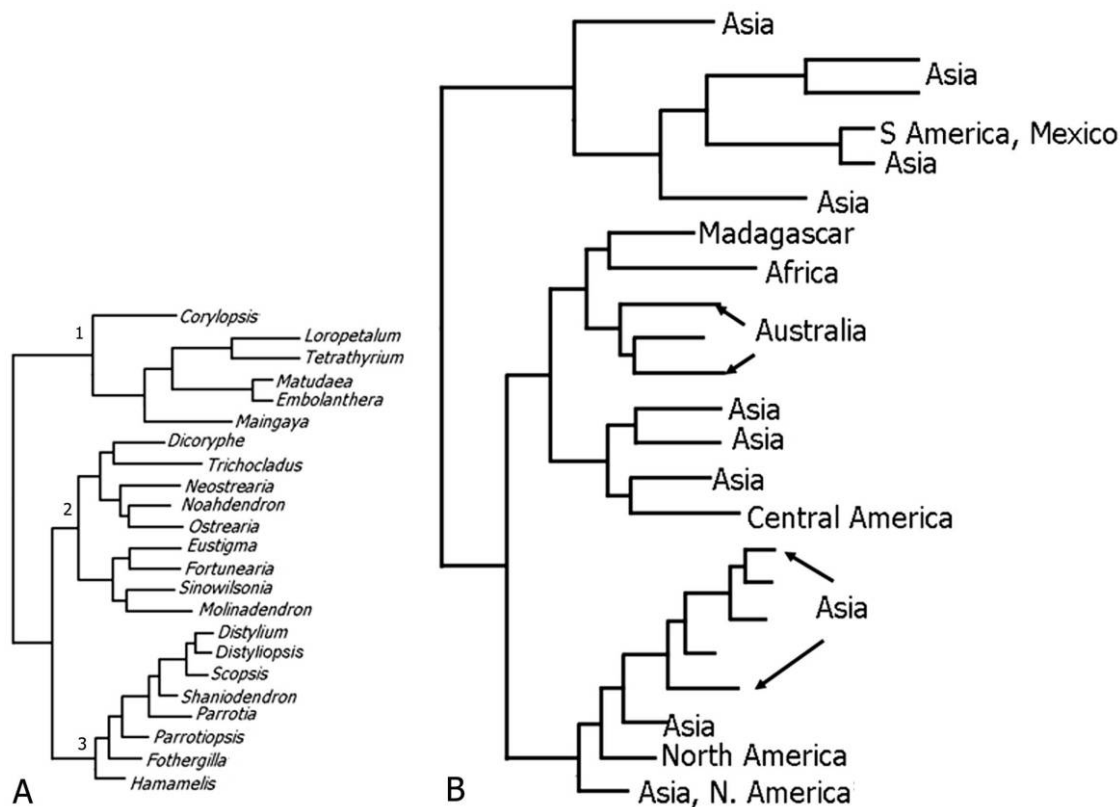
Fig. 1 *A*, Phylogenetic relationships based on morphological and molecular analysis (modified from Li and Bogle 2001). 1 = loropetalid, 2 = eustigmatid, and 3 = fothergillid clades. *B*, Biogeographic distribution of taxa mapped on phylogeny (see *A*). Modified from Li and Bogle (2001).

known from many Tertiary localities (Hu and Chaney 1940; Suzuki 1961; Koch 1963; Wolfe and Wehr 1987; Meyer and Manchester 1997; Radtke et al. 2005).

In this study, we describe *Hamawilsonia boglei* Benedict, Pigg & DeVore gen. et sp. nov., a distinctive infructescence from the Late Paleocene Almont flora of central North Dakota. Infructescences are elongate spikes that are most similar to the extant Asian endemic genus *Sinowilsonia*, fruit morphology is most like that of *Hamamelis*, and seed anatomy is a mosaic of several extant genera. *Hamawilsonia*'s affinities with *Sinowilsonia* are further supported by the presence of associated pollen catkins with distinctive in situ tricolpate reticulate pollen assignable to the sporae dispersae taxon *Retitrescolpites catenatus* Pocknall & Nichols. *Hamawilsonia* is a Late Paleocene genus with a combination of characters not seen in any single hamamelid taxon today, and it documents another Almont taxon with strong North American–Asian affinities.

Material and Methods

Fossils occur at the original Almont site in Morton County, North Dakota, in a silicified shale that preserves both the morphological form and anatomical structure of fruits and seeds. These fossils are part of a diverse flora of ∼30 families and 50 genera (Crane et al. 1990; Pigg and DeVore 2005; Pigg et al. 2006; Taylor et al. 2006). Stratigraphically, the Almont flora

occurs within the Sentinel Butte Formation and is considered Late Paleocene (Tiffanian 3) in age, based on correlations of molluscan faunas with known North American Land Mammal Ages (Kihm and Hartman 1991). Interestingly, we have not yet found hamamelid remains in the floristically similar Beicegel Creek locality in western North Dakota (Manchester et al. 2004; Pigg and DeVore 2005).

Fruits were photographed from fractured surfaces and then embedded in Bio-Plastic synthetic resin (Ward's Natural Science, Rochester, NY) and wafered on a Buehler Isomet 1000 saw (Lake Bluff, IL) into sections 0.4–1.0 mm thick. The sections were mounted on slides, ground down to a minimal thickness, and photographed using reflected and transmitted LM. Extant fruits and seeds were also embedded in Bio-Plastic, sectioned with a lapidary saw, and photographed in the same manner as the fossils. Extant specimens of *Sinowilsonia* were obtained from the Zurich Botanical Garden and the Arnold Arboretum. Selected fossil and extant specimens were studied by SEM using either a Hitachi (Tokyo) S-415A at 15 kV, with a 20-nm gold coating (fruits, seeds) or a Leica-Cambridge (Structure Probe, West Chester, PA) Stereoscan 360FE at 10 kV, with a 20-nm gold coating (in situ pollen in catkins).

Specimens of *Hamawilsonia boglei* are housed at the Field Museum, Chicago (FMNH; specimens prefixed PP); the Florida Museum of Natural History, Gainesville (UF; prefixed IU and UFLM); the University of Wisconsin–Stevens Point (UWSP); and Arizona State University, Tempe (ASU). Terminology follows

that of Li (1997), Meyer (2003), and Zhang et al. (2003), except where noted.

Systematics and Description

Family—Hamamelidaceae *R. Br.*

Subfamily—Hamamelidoideae *Reinsch*

Genus—Hamawilsonia *Benedict, Pigg et DeVore gen. nov.*

Type Species—Hamawilsonia boglei *Benedict, Pigg et DeVore gen. nov. (Fig. 2; Fig. 3A, 3C–3F; Fig. 4A, 4B, 4D, 4F–4I; Fig. 5A, 5E, 5F)*

Generic diagnosis. Infructescence a spike; fruits sessile, borne alternately on thick, elongate axis, cuboidal-ovoid, bilocular; locules ellipsoid to ovoid; styles paired, persistent, relatively short, recurved; style base enlarged into thickened ridge; main vascular bundles within exocarp two, positioned between locules; endocarp sclerified, composed of two layers; dehiscence septicidal and ventricidal, one seed per locule, ellipsoid to slightly obovate.

Species diagnosis. At least 20 fruits per infructescence, infructescence axis up to 9.2 cm long × 0.5 cm wide; fruits 10–12 mm long × 10–12 mm wide, locules 5–10 mm long × 3–5 mm wide; styles up to 2 mm long; endocarp with outer layer of tangentially elongated cells, 35–50 cells thick, inner layer of radially elongated cells, approximately one cell thick; seeds 7 mm long × 4 mm wide; elliptical to slightly obovate, seed coat

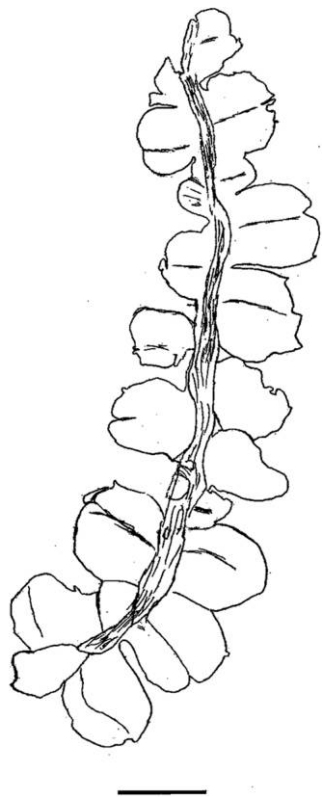**Fig. 2** Line diagram of holotype of *Hamawilsonia boglei* gen. et sp. nov. Redrawn from UWSP 898; ×1.3. Scale bar = 1 cm.

composed of three distinct cell layers, outermost layer of large cuboidal to radially elongate thick-walled cells, uniseriate; central zone of smaller sclerotic cells grading from radially elongate to isodiametric centrally and tangentially elongate to the inside, eight to 12 cells thick; innermost zone of tangentially elongate cells, three cells thick.

Prior citation. Hamamelidaceae. Crane et al. (1990), pp. 37–39, fig. 15A–15E.

Locality. Almont, North Dakota (Crane et al. 1990).

Stratigraphy. Sentinel Butte Formation, Late Paleocene.

Holotype. UWSP 898 (figs. 2, 3A).

Paratypes. PP 34417a (fig. 3C; also fig. 15D of Crane et al. [1990]); ASU HAM 7 (fig. 3D); PP 45513a, b (fig. 3E); UWSP 3585 (fig. 3F); IU 1015722–5977 (fig. 4A; also fig. 15A, 15B of Crane et al. [1990]); PP 34476a, b (fig. 4B); UWSP 4352 (fig. 4D, 4F); ASU HAM 4 (fig. 4G); PP 45515a, b (fig. 5A, 5E, 5F). Not figured: ASU HAM 1–3, 5–6, 8–11; GSCU HAM 1; IU 15722–5978 (illustrated in fig. 15C, 15E of Crane et al. [1990]); PP 45514, 45517–20, 45522–7, 45529–35, 45537–45; UF 15722–15510, 22348–9, 22351–3, 22364, 22408; UWSP 3316, 3584, 3675, new 1, new 2.

Etymology. The generic name *Hamawilsonia* indicates close affinities of this fossil to a combination of the disjunct witch hazel genus *Hamamelis* and the Asian endemic genus *Sinowilsonia*. The species name *boglei* is in honor of A. Linn Bogle in recognition of his numerous contributions to the study of Hamamelidaceae.

Description of Hamawilsonia. The description of *H. boglei* is based on observations from 15 specimens of infructescences and 90 isolated fruits. Of these, 12 infructescences and 20 individual fruits were studied in detail. Infructescences are elongate spikes with up to 20 fruits (figs. 2, 3A). The longest infructescence has a thick axis 9.2 cm long × 0.5 cm across (fig. 3C). Fruits are densely attached alternately along the axis and are clustered toward the apex (fig. 2; fig. 3A, 3C). Three specimens bear numerous structures 2–3 mm across (the "small blisters" of Crane et al. [1990]) that may represent either aborted gynoecia or their attachment scars (fig. 4D, 4F).

Mature biloculate fruits are cuboidal-ovoid in outline and 10–12 mm across, with a convex distal face and persistent, paired recurved styles up to 2 mm long (fig. 4A, 4B). At the base of each persistent style, the outer exocarp tissue of the fruit is often expanded into a thickened ridge (fig. 4A, 4B). No obvious calyx is present on specimens, and it is unclear whether it was lacking in life or lost through poor preservation. Locules are ~5–10 mm long × 3–5 mm wide and appear elliptical to ovoid in transverse section. They show a combination of septicidal and ventricidal dehiscence (fig. 4A, 4B, 4G).

Fruit walls are two-layered, with an exocarp that is usually present but often is poorly preserved and a well-preserved, sclerenchymatous endocarp (fig. 4H, 4I). The endocarp is composed of two distinct layers, an outer region 35–50 cells thick with tangentially oriented, thick-walled, sclerotic cells that are up to 340 μm long × 30 μm wide (fig. 4I) and an inner uniseriate layer with radially elongate cells 20 μm high × 10 μm wide that appear cuboidal in transverse section (fig. 4H).

Most of the fruits appear to be senescent structures that have already dehisced (fig. 4A, 4B, 4G) and are infilled with mud, producing locule casts that fill the position originally occupied by the seeds. However, intact seeds have been found
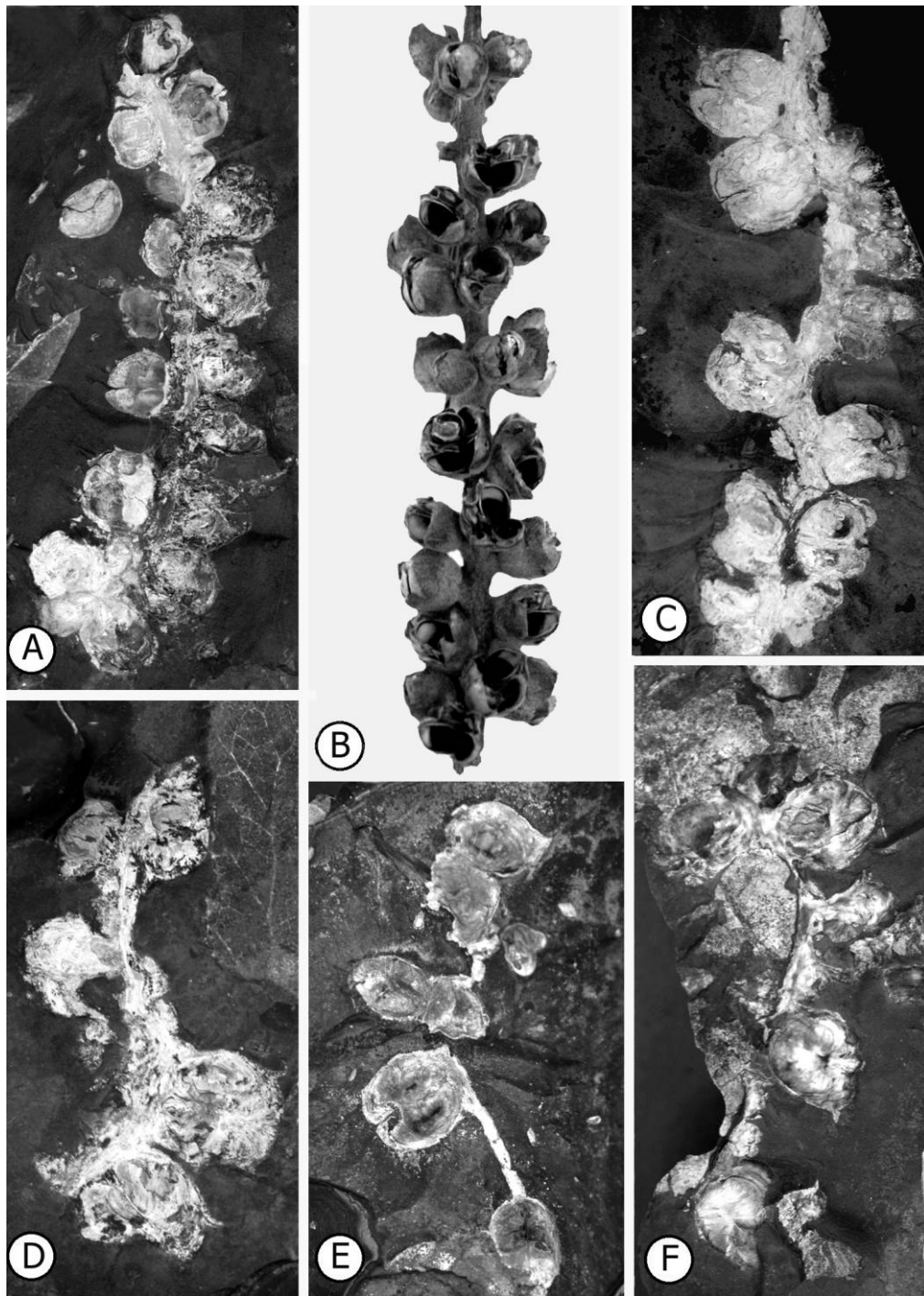
Fig. 3 Infructescences of *Hamawilsonia* gen. nov. and extant *Sinowilsonia*. *A*, *C–F*, *Hamawilsonia*; *B*, *Sinowilsonia*. *A*, Holotype showing densely arranged, sessile fruits on axis. Fruits are most densely clustered at the tip of infructescence (at bottom); UWSP 898; ×1.1. *B*, Mature infructescence of extant *Sinowilsonia henryi* showing dense arrangement of sessile fruits; ×1. *C*, Surface fracture of *Hamawilsonia* infructescence showing sessile arrangement of fruits, which become more densely clustered toward apex (at bottom). PP 34417a; ×1. *D*, Surface fracture of specimen bearing four fruits. The uppermost fruit is crushed, with both locules split apart; ASU HAM 7; ×1.4. *E*, Surface fracture showing overall arrangement of fruits on infructescence. The fruit at the center of the axis shows two ovoid locules covered by traces of exocarp tissue; PP 55113a; ×0.9. *F*, Surface fracture showing five helically arranged, attached fruits; UWSP 3585a; ×1.1.
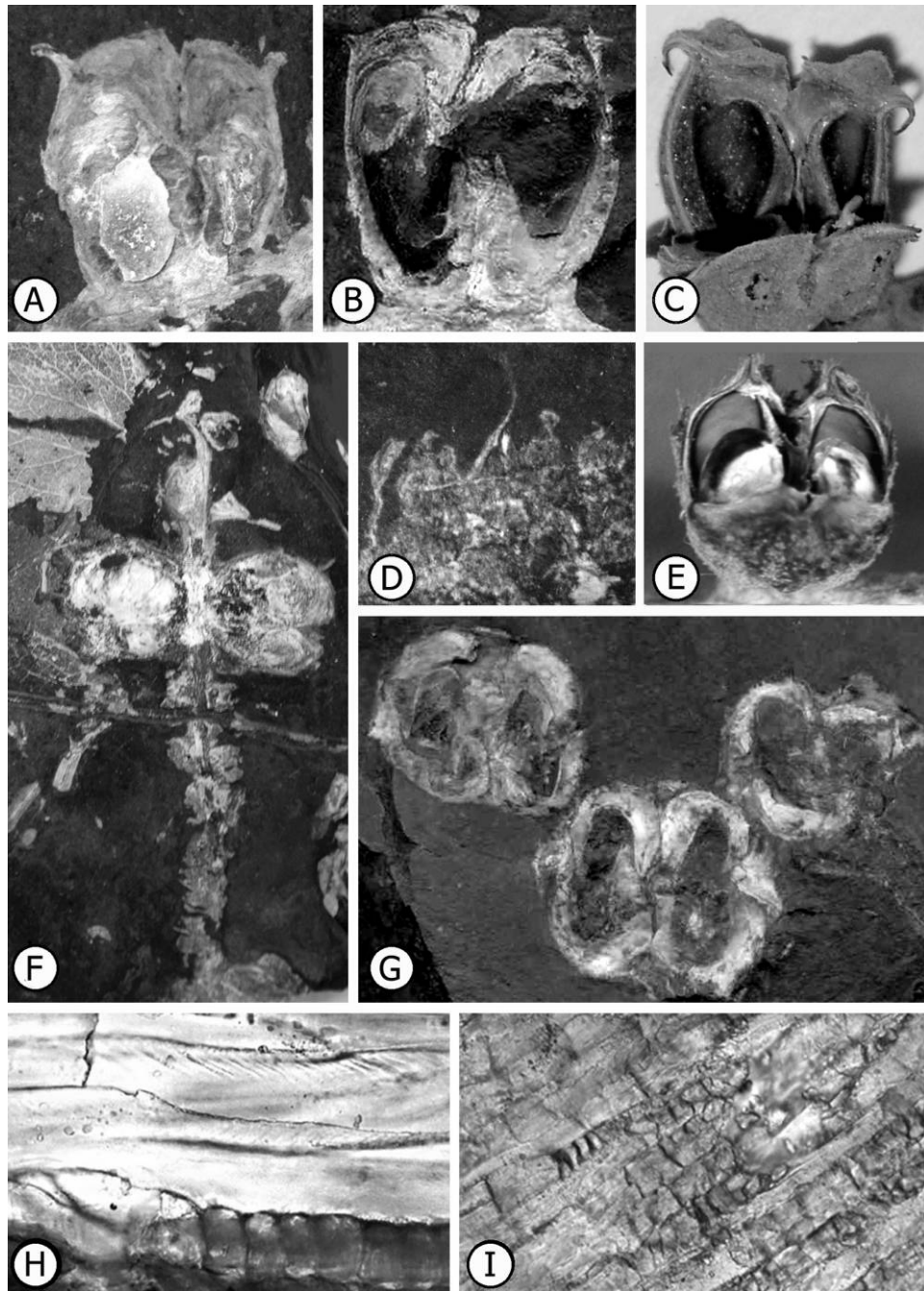
Fig. 4 Fruit morphology of *Hamawilsonia*, *Hamamelis*, and *Sinowilsonia*. *A*, *B*, *D*, *F*, *G–I*, *Hamawilsonia*; *C*, *Hamamelis*; *E*, *Sinowilsonia*. *A*, Fruit showing cuboidal shape and paired, persistent styles; IU 15722–5977; ×3.2. *B*, Fruit showing locules that are infilled with mud; PP 34476; ×3.3. *C*, Extant *Hamamelis* fruit with cuboidal shape and paired persistent styles; ×3.3. *D*, Close-up of specimen in *F* showing presumably abortive fruits. Note possible calyx band and style; UWSP 4352; ×8.5. *E*, *Sinowilsonia* fruit with ovoid shape; ×3.6. *F*, Infructescence showing several small, presumably abortive fruits, with two well-developed fruits; UWSP 4352; ×1.6. *G*, Three fruits showing cuboidal shape in transverse section; ASU HAM 4; ×3.0. *H*, Anatomical structure of endocarp wall showing outer tangentially aligned sclerotic cells and inner, uniseriate radial layer; ×470. *I*, Anatomical structure of endocarp wall showing outer tangentially aligned sclerotic cells; ×188.

in two fruits (fig. 5A, 5E). Seeds are 7 mm long × 4 mm wide and ellipsoid, almost completely filling the locule (fig. 5A).

The seed coat is 450 μm thick, with three zones (fig. 5F). The outermost zone is made up of a uniseriate layer of large,

radially elongate thick-walled cells 72.5 μm high × 30 μm wide, each with a large lumen up to 50 μm high × 22 μm wide. The central zone, which makes up the bulk of the seed coat, is 12 cells thick. Cells are thick walled, sclerotic, and
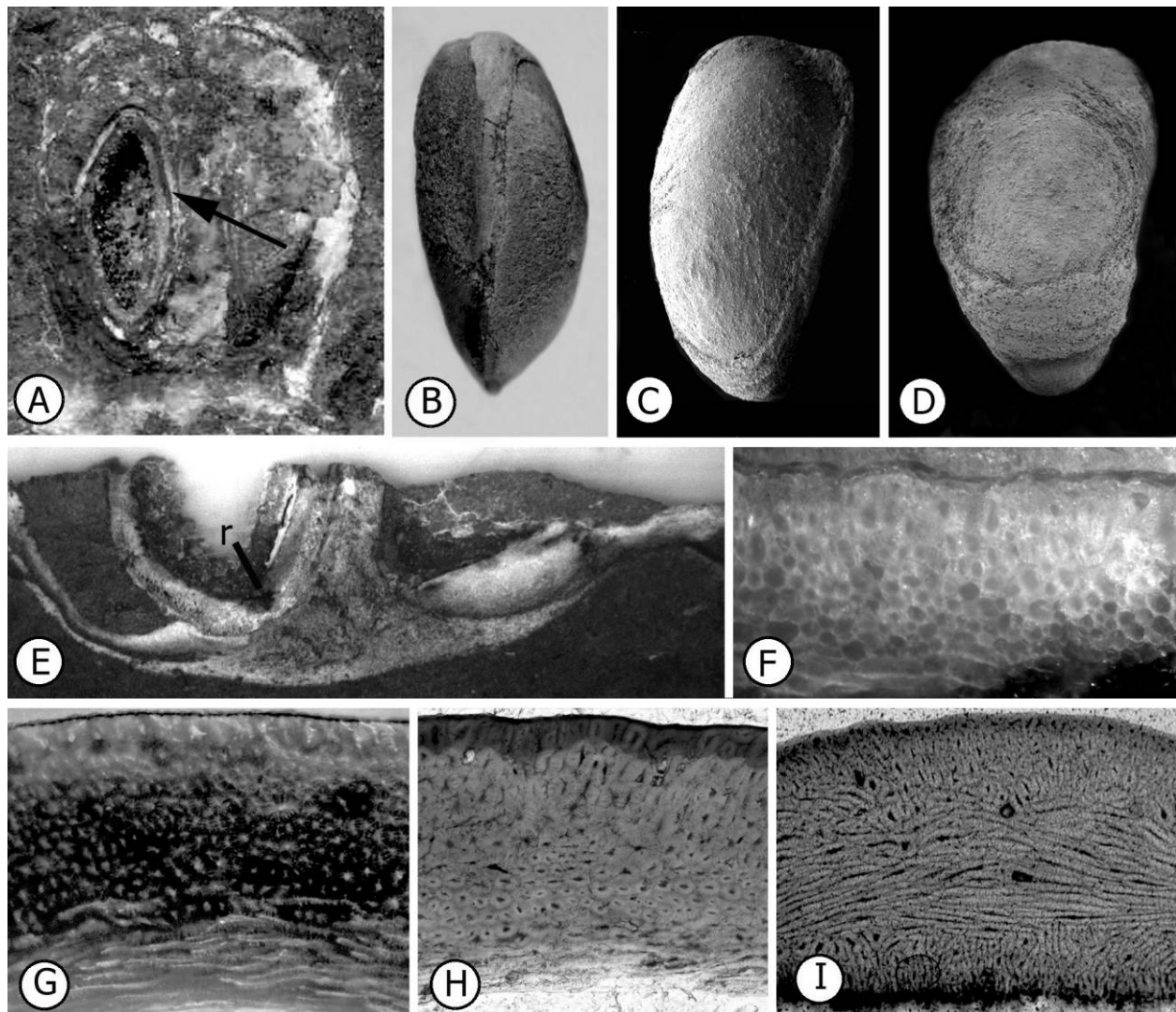
Fig. 5 Seeds of *Hamawilsonia*, *Corylopsis*, *Hamamelis*, *Sinowilsonia*, and isolated asymmetric seeds in Almont matrix. *A*, *Hamawilsonia* fruit showing a seed within locule (arrow); PP 45515; ×4. *B*, Isolated asymmetric seed showing general seed shape and position of micropyle and raphe; IU 6967; ×6.8. *C*, SEM of isolated seed; ×7.4. *D*, SEM of isolated seed; ×7.1. *E*, Cross section of fruit in fig. *3A* showing placement of the seed. Note black tissue of the raphe to the inside of the seed coat (*r*); PP 45515; ×6.7. *F*, Seed coat of *Hamawilsonia* in transverse section showing the tissue layers. Top layer corresponds to the outermost layer of the seed coat; PP 45515; ×72. *G*, Seed coat of *Hamamelis* in transverse section; ×120. *H*, Seed coat of *Corylopsis* in transverse section; ×125. *I*, Seed coat of *Sinowilsonia* in transverse section; ×125.

generally smaller than the cells of the outermost layer. Cells within this entire zone grade from somewhat small (18×20 μm), radially aligned cells to the outside to larger isodiametric to tangentially elongate cells that are 32.5×42.5 μm toward the inside. The innermost zone is made of tangentially elongate cells, about three cell layers thick, 22.5 μm high, and 235 μm wide. This layer is the most poorly preserved of the three and is sometimes lacking. The endosperm and embryo are not preserved.

Approximately six seed casts showing similar morphology to the in situ seeds have been found isolated within the Almont matrix. They are ellipsoid, 7 mm long × 3 mm wide, and have a prominent hilar scar over the micropylar end (fig. 5B–5D). The scar is ovoid and is positioned apically, extending

slightly down the side. The seeds also show a distinct indentation on the inside of the seed coat that presumably relates to the positioning of the raphe (fig. 5D).

Associated pollen catkins and pollen. Of the several types of pollen catkins that occur at Almont, several have been found that contain characteristic hamamelid pollen (fig. 6). These staminate catkins are ~2.5 cm long × 0.8 cm wide, with loosely arranged florets along a lax inflorescence axis (fig. 6A). The structure of catkins is not studied in detail in this article. In situ pollen recovered from the catkins (fig. 6B–6E) is referable to the sporae dispersae taxon *Retitrescolpites catenatus* Pocknell & Nichols (1996). It is 21.6 μm in diameter and tricolpate, with a distinctive reticulate pattern of large and small luminae and heterobrochate muri (fig. 6C, 6E).
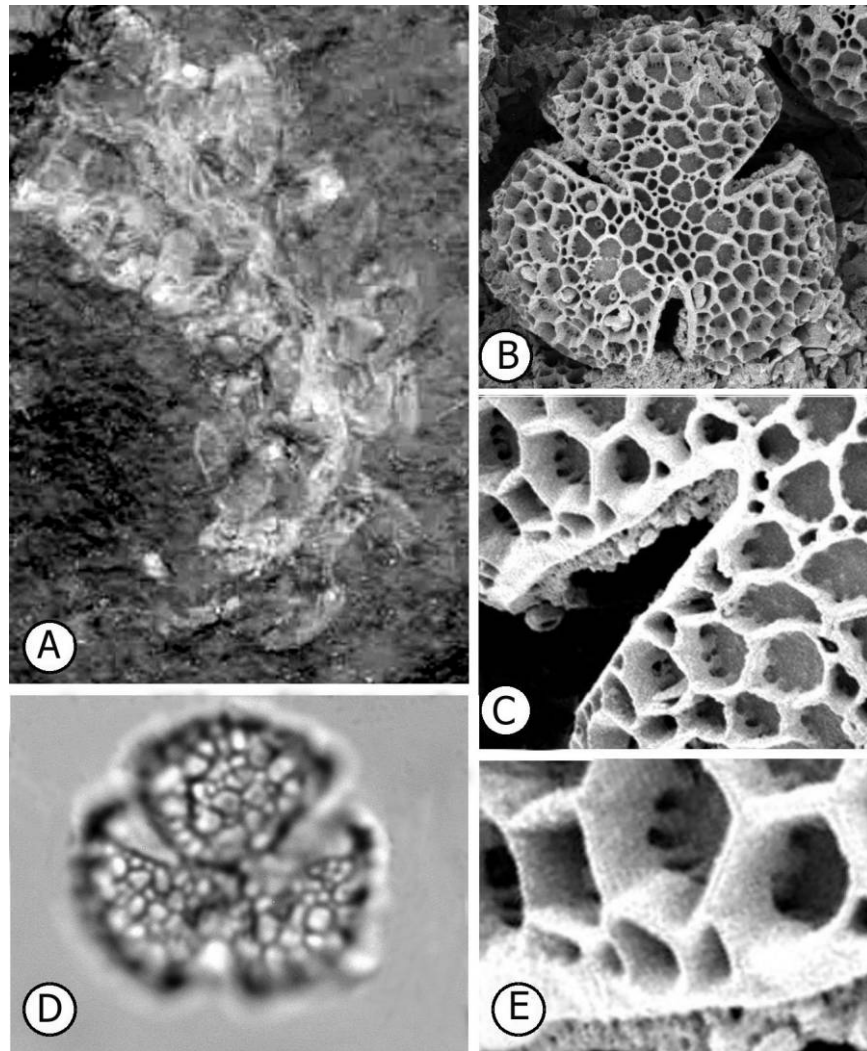
Fig. 6 Hamamelid pollen catkins and in situ pollen. *A*, Catkin with in situ pollen; PP 45551; ×20. *B*, SEM of individual in situ pollen grain found within a catkin; ×2000. *C*, SEM detail of *B* showing reticulate exine and part of aperture; ×5692. *D*, LM of individual pollen grain found in matrix; ×2000. *E*, Detail of reticulate ornamentation of exine; ×8538.

Discussion

Taxonomic Placement of Hamawilsonia

Hamawilsonia boglei is a distinctive infructescence that clearly belongs to the Hamamelidaceae, subfamily Hamamelidoideae (Endress 1989*c*; Li 1997). Family-level characters include infructescences in spikes, racemes, or clusters; bilocular fruits with a leathery exocarp and sclerified endocarp, often persistent styles; and ventricidal or ventricidal and septicidal dehiscence (see Ickert-Bond et al. 2007). Within the subfamily Hamamelidoideae, synapomorphies include the "explosive" dispersal mechanism of seeds and the presence of a single hard, ellipsoid, ovoid, or obovoid seed per locule, which is required for the mechanism to function properly (Endress 1989*a*, 1989*c*; Li 1997).

Because the Almont fossils show features in a combination that is unlike that of any other taxon of extant or fossil Hamamelidoideae, we are assigning them to a new genus. We chose the name *Hamawilsonia* to emphasize the fossils' mosaic nature, with closest similarities to *Hamamelis* and the Chinese endemic genus *Sinowilsonia* (fig. 3*B*). Infructescences are most similar to those of *Sinowilsonia*, being spikes with numerous sessile fruits borne alternately on a stout, elongate axis (fig. 2; fig. 3*A*, 3*C*). In contrast, infructescences of *Hamamelis* have a short axis, ~3 cm long, and each bears one to five (typically three) fruits (Shoemaker 1905; Li 1997; Li and Bogle 2001; Anderson and Hill 2002; Meyer 2003). Fruit morphology of *Hamawilsonia* is similar to *Hamamelis* in size and shape (fig. 4*A*–4*C*). Fruits of both genera are characteristically cuboidal to ovoid in outline to slightly obovoid, in contrast to the more typically ovoid to obovoid forms. The base of each style is expanded into a distinctive thickened ridge (4*A*–4*C*). This feature appears to be well pronounced only in *Hamawilsonia* and *Hamamelis* (fig. 4*A*, 4*C*; fig. 7*A*) and slightly developed in *Corylopsis* (fig. 7*C*).
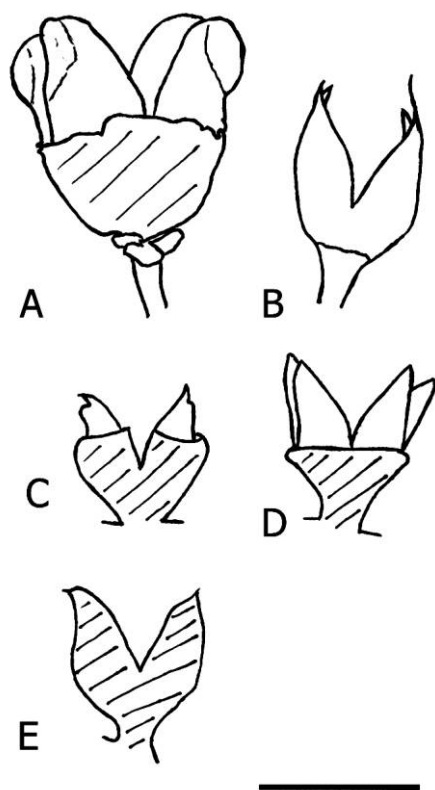
Fig. 7 Comparison of selected fruits within the Hamamelidoideae drawn in dorsal view with septicidal and ventricidal dehiscence shown. *A*, *Hamamelis* sp. *B*, *Distylium racemosum*. *C*, *Corylopsis* sp. *D*, *Fothergilla* sp. *E*, *Sinowilsonia henryi*. Oblique lines represent persistent calyx tissue except in *S. henryi*, where they represent a persistent floral cup. Tissue without lines represents exocarp tissue. Scale bar = 1 cm.

The only fossil infructescence with known anatomical structure available for comparison with *Hamawilsonia* is the middle Eocene *Fortunearites endressii* Manchester from the Clarno Nut Beds of central Oregon (Manchester 1994). *Fortunearites* is similar to *Hamawilsonia* in having sessile, biloculate fruits and in details of seed morphology. The infructescence of *Fortunearites* is significantly smaller (5.3 cm long) and has a denser, more compact arrangement of fruits (15 per axis). The fruits are essentially half the size of *Hamawilsonia* fruits (5–7 mm long). Seed morphology and size also differ between these two fossils. Manchester (1994) reported that vascular bundles in *Fortunearites* curve over the base of the seed to produce a straplike ridge on the seed coat, a character not observed in *Hamawilsonia*.

Evacarpa Maslova and Krassilov, a genus established for Paleocene inflorescences and infructescences from Kamchatka, in far eastern Russia, was compared to both Platanaceae and Hamamelidaceae (Maslova and Krassilov 1997). These impression fossils show a characteristic bilocular fruit type similar to those of Hamamelidaceae that are clustered into capitula of ~16 fruits, in a manner similar to pistillate structures of Altingiaceae. These fossils are apparently related to Altingiaceae; however, their limited preservation restricts detailed comparison.

Additional circumstantial evidence for the affinities of *Hamawilsonia* is based on the co-occurrence at Almont of associated pollen catkins (fig. 6*A*) with in situ tricolpate, reticulate hamamelid pollen (fig. 6*B*–6*E*). It is particularly interesting that hamamelid pollen catkins occur within this matrix along with the *Hamawilsonia* infructescences, since most genera in Hamamelidoideae have bisexual flowers and *Sinowilsonia* is the only genus that consistently produces separate pollen catkins (Li 1997). (Several other genera, including *Fortunearia*, *Parrotia*, and *Sycopsis* are reported to be andromonoecious [table 1; Endress 1993; Li 1997].) There is no evidence of stamens on *Hamawilsonia* fruits; however, this feature would probably not be preserved in the fossil, since even within extant genera such as *Hamamelis*, the mature fruits lack them.

All genera in Hamamelidaceae sensu stricto have tricolpate, reticulate pollen (Zavada and Dilcher 1986). However, details of the ornamentation as seen with SEM are taxonomically diagnostic (Bogle and Philbrick 1980). The pattern seen in the in situ pollen is most similar to that of pollen from the extant genera *Sinowilsonia* and *Fortunearia* (Bogle and Philbrick 1980), particularly in the pattern and distribution of large and small lumina as well as the presence of heterobrochate muri. This pollen type fits most closely in the sporae dispersae taxon *Retitrescolpites catenatus* (Pocknall and Nichols 1996).

The genus *Retitrescolpites* is used for dispersed tricolpate pollen with reticulate lumina larger than 1 μm. The species *R. catenatus* is distinguished by lumina that finely grade toward the smooth sides of the colpal margins as well as the combination of large and small lumina, while others have more consistent, larger lumina. Two other species of *Retitrescolpites* occur rarely in the matrix at Almont. *Retitrescolpites anguloluminosus* (Anderson) Frederiksen 1979 is similar to *R. catenatus* except that the heterobrochate muri that characterize *R. catenatus* are lacking in *R. anguloluminosus* and a third type, currently designated as *Retitrescolpites* sp. (M. Farabee, unpublished data). It is unclear whether these sporae dispersae grains are of hamamelid or some other taxonomic affinities.

Does Explosive Dehiscence Constrain Morphology?

One of the strongest synapomorphies that unites members of subfamily Hamamelidoideae is explosive dehiscence (Endress 1989*a*; Li 1997; Magallón 2007). The functioning mode of this mechanism is related to the morphology of the fruit wall in the group. For the fruit to eject the seeds effectively (and in a relatively precise parabolic motion), the fruit wall is structured in a manner that will promote a pinching of the base of the seed, resulting in ejecting the seed. The force applied to the base of the seed is generated via xerochastic movement when the mature fruit wall dries. The desiccation of the fruit wall alters the shape of the bilocular fruit so that the endocarp acts as a pair of tongs that squeezes the base of the seed (Eichholz 1886; Endress 1989*a*).

This mechanism of explosive dehiscence in Hamamelidoideae is analogous to the rifled barrels in firearms (Nonte 1973, pp. 214–215). To increase precision, accuracy, and distance, the inside of a gun barrel is grooved in a twin helical pattern (typical in long-barreled rifles) or a polygonal, often

Table 1

Features of Infructescence and Fruit Type in Hamamelidoideae Based on Endress's (1989b) Classification

Tribe, subtribe, genus (no. species)	Sex distribution	Infructescence (inflorescence)	No. fruits	Fruit shape	Style persistence, length (mm)	Calyx persistence, length
Hamamelidoideae, Hamamelidineae:						
Hamamelis (5)	Bisexual	Clustered spike	3–5	Ovoid to cuboidal	Yes, short	Yes, 1/2 of fruit
Loropetalinae:						
Embolanthera (2)	Bisexual	Spike/raceme	?	?	?	?
Loropetalum (1–3)	Bisexual	Terminal raceme to spike	6–8[a]	Ovoid-globose-obovoid	?, very short	Yes, 2/3–1/2 of fruit
Maingaya (1)	Bisexual	Terminal raceme	2	Ovoid	No?	Yes, 1/2 of fruit
Tetrathyrium (1)	Bisexual	Spike		Ovate-orbicular	?	Yes
Dicoryphinae:						
Dicoryphe (13)	Bisexual	Spike	2	Ovoid?	?	?
Trichocladus (5)	Bisexual	Terminal cluster	?	Subglobose	Sometimes	?
Neostrearia (1)	Bisexual	Spike	?	Obovoid	No?	Yes, 1/2 of fruit
Noahdendron (1)	Bisexual	Spike	50	Ovoid?	Yes	?
Ostrearia (1)	Bisexual	Spike	?	Obovoid	No	Yes, 1/3–1/2 of fruit
Corylopsidaeae:						
Corylopsis (7–20)	Bisexual	Spike/raceme	Varies	Ovoid-globose	Yes, long	Yes, 1/2
Eustigmateae:						
Eustigma (2)	Bisexual	Terminal raceme	?	Ovoid-globose	Yes? very short?	No?
Fortunearia (1)	Andro-monecious	Raceme	~6	Ovoid-globose	?	Yes, 1/2 of fruit
Sinowilsonia (1)	Unisexual	Spike	~60	Ovoid-globose	No	Yes, covers fruit
Fothergilleae:						
Distyliopsis (6)	Andro-monecious	Terminal raceme	"Few"[a]	Ovoid?	Yes, very short	Yes, covers fruit
Distylium (18)	Andro-monecious	Terminal raceme	1–3	Ovoid-globose	Yes, 2–4	No
Embolanthera (2)	Bisexual	Spike/raceme	?	?	?	?
Fothergilla (2)	Bisexual	Spike	3+	Ovoid	Yes	Yes or no; if yes, 1/2 of fruit
Matudaea (2)	Bisexual	Spike or panicle	?	Oblong-ovoid	No?	No
Molinadendron (3)	Bisexual	Spike	?	Ovoid?	Yes?	?
Parrotia (1)	Andro-monecious	Spike	3–7[a]	Long-globose	Yes, 5	?
Parrotiopsis (1)	Bisexual	Clustered	?	Ovoid?	No	?
Sycopsis (9)	Andro-monecious	(Racemes) spikes	3–6	Ovoid-globose	Yes or no, 2–4	Yes, covers fruit
Trichocladus (5)	Bisexual	Terminal cluster	?	Subglobose	Sometimes	?
Hamawilsonia (1)	Unisexual	Spike	20	Cuboidal	Yes	No?
Fortunearites (1)	Unisexual	Spike	15	Cuboidal	?	?

Sources.   Lundell 1940; Vink 1957; Smith 1958; Verdcourt 1971; Hewson 1981; Endress et al. 1985; Manchester 1994; Dorr 2001; Anderson and Hill 2002; Brummitt and Utteridge 2003; Meyer 2003; Zhang et al. 2003, Magallón 2007; J. Benedict, personal observation.

[a] Information from flower or inflorescence.

octagonal pattern (common in short-barreled handguns). Both patterns cause a narrowing of the lateral spin of the fired bullet, increasing the precision and accuracy and translating the energy into a longer-distance trajectory. The fruits of Hamamelidoideae achieve a type of rifling similar to that in short-barreled guns by having in the endocarp lining of the fruit a single layer of cells that are oriented in the same direction the seed will travel. This explosive dehiscence mechanism may be of particular value to fruit dispersal in the Hamamelidoideae, as these plants typically are small trees and shrubs of the subcanopy layer, where wind dispersal of seeds is rare (Howe and Smallwood 1982).

Many authors have remarked on the uniform morphology of fruits in subfamily Hamamelidoideae and have suggested that the mechanism of explosive dehiscence has deeply constrained possible variation (Endress 1989a, 1993; Grote 1989; Zhang and Wen 1996; Magallón 2007). Although the assumption has been that fruits within the subfamily are quite similar,

there has been little comparative morphological study of fruit variation (Magallón 2007). Our preliminary survey of this group reveals that while the features essential for explosive dehiscence (a single, hard, smooth elliptical seed per locule, basally tapered fruits, and anatomical structure where endocarp splits from exocarp) are consistent throughout the subfamily, there is more variation present in other features than has been recognized generally (tables 1, 2).

A complete analysis of the variation present within the subfamily is beyond the scope of this article; however, we note several features of infructescences, fruits, and seeds that we believe are of potential, yet mostly untapped, taxonomic value (table 1; fig. 7). Several of these features have been noted previously by Endress (1967, 1970, 1989b). Variations in infructescence include (1) infructescence type, (2) sex distribution, (3) length and thickness of infructescence axis, (4) number of fruits, and (5) presence or absence of lenticels on fruits. Variations of fruit morphology include (6) shape, (7)

Table 2
Seed Coat Anatomy for Selected Genera of Hamamelidoideae

	Corylopsis	*Distylium*	*Hamamelis*	*Sinowilsonia*	*Hamawilsonia*
Seed coat width (μm)	320	350	350	320	450
Exotesta:					
Cell number	1	1	1	1	1
Orientation	Cuboidal-palisade	Cuboidal	Cuboidal-palisade	Cuboidal	Cuboidal-palisade
Cell height × width (μm)	45 × 30	25 × 20	70 × 47.5	20 × 20	72.5 × 30
Mesotesta:					
Total cell number	9	9	12–13	18	8
Outer cell number	2–3	2–3	na	6	4
Orientation	Radial	Radial	Interspersed radial and tangential	Radial with a few tangential	Radial
Cell height × width (μm)	35 × 25	42.5 × 30	25 × 22.5 (r) 22.5 × 67.5 (t)	27.5 × 30	20 × 18
Inner cell number	6–7	6–7	na	12	4
Orientation	Radial	Radial	Interspersed radial and tangential	Tangential	Radial
Cell height × width (μm)	20 × 18	. . .	25 × 22.5 (r) 22.5 × 67.5 (t)	20 × 195	42.5 × 32.5
Endotesta:					
Cell number	2–4	10	8	2–5	3–5
Orientation	Tangential	Tangential	Tangential	Radial	Tangential
Cell height × width (μm)	22.5 × 160	27.5 × 235	32.5 × 210	20 × 15	22.5 × 235

Sources.   Netolitzky 1926; Melikian 1973; Rao 1974; Corner 1976; Manchester 1994; Zhang and Wen 1996; this study. r = radial; t = tangential; na = not applicable.

presence/absence and features of persistent styles, (8) persistence of the calyx, (9) ratio of calyx length to fruit length, and (10) shape of the fruit apex. Additional characters yet to be comprehensively studied include (11) detailed seed morphology and (12) seed coat anatomy.

Some of these features seen in the infructescence are comparable to those of the inflorescence, while others are specific to mature infructescences. For example, the number of flowers produced in an inflorescence limits the maximum number of fruits that can be present, yet not all flowers develop into fruits. Since *Disanthus* (Hamamelidaceae, subfamily Exbucklandoideae) has two flowers per fruit, it could not have more than two fruits per infructescence; *Hamamelis* could not have more than five (Anderson and Hill 2002). Additionally, internodal elongation occurs during later stages of fruit development and is independent of inflorescence length.

1. *Infructescence type.*   Infructescence type varies from spikes to racemes to occasionally clustered fruits (headlike spikes; table 1). Spikes occur in *Sinowilsonia*, *Fothergilla*, and some species of *Corylopsis*, while *Eustigma*, *Fortunearia*, and *Fortunearites* have racemes. *Parrotiopsis* and *Trichocladus* both have a short fruiting axis only a few centimeters long, with typically headlike spikes. *Embolanthera* has been interpreted as having either racemes or spikes. This feature can be variable at the species level within *Corylopsis*.

2. *Sex distribution.*   Infloresences (and infructescences) of Hamamelidoideae are most typically bisexual (table 1) but are occasionally andromonoecious and, more rarely, unisexual (Endress 1967, 1970, 1989b; Magallón 2007). This is of particular interest to us, since the finding of pollen catkins with hamamelid pollen in association with *Hamawilsonia* can be inferred to indicate a similarity with extant *Sinowilsonia*.

3. *Thickness and length of infructescence axis.*   The infructescence axis can be slender to thick and elongate to extremely short. The axis is elongate in *Sinowilsonia* (up to 20 cm) and sometimes in *Fothergilla* (Meyer 2003) but short (a few centimeters) in *Hamamelis*, *Parrotia*, and *Parrotiopsis*.

4. *Number of fruits per infructescence.*   An infructescence of *Hamamelis* never has more than five fruits (Anderson and Hill 2002). *Fothergilla* fruits occur in groups of more than three; *Dicoryphe* and *Maingaya* are characterized by two fruits per infructescence (table 1). In contrast, *Sinowilsonia* and *Corylopsis* have elongate spikes with a variable number of fruits per spike (up to 60 in *Sinowilsonia*).

5. *Lenticels.*   Lenticels have been reported on fruits of *Fortunearia* and *Eustigma* (Endress 1989a; Zhang et al. 2003), indicating that it may be a synapomorphy for the eustigmatid clade.

6. *Fruit shape.*   The fruit shape ranges from ovoid (*Loropetalum*, *Fothergilla*) to obovoid-globose (*Sycopsis*) to obovoid (*Neostrearia*) to cuboid (*Hamamelis*). It is interesting that while most of the fruits are ovoid to obovoid (table 1), only *Hamamelis* and the fossil *Hamawilsonia* vary from ovoid to a notably cuboidal or square shape (figs. 4A–4C, 7).

7. *Persistent styles.*   Persistent styles (stylar beaks) are common in Hamamelidoideae. Styles vary in length and shape. They are elongate and showy in *Corylopsis*, are of intermediate length in *Hamamelis*, and are not present in *Parrotiopsis*. In some genera (e.g., *Corylopsis*), styles are straight; in others, such as *Hamamelis*, they are recurved (table 1).

8. *Persistence of the calyx.*   Most of the genera have a persistent calyx (fig. 7A, 7C, 7D). Only a few (e.g., *Parrotia*) apparently lack a calyx on maturity (fig. 7B; table 1).

9. *Ratio of calyx-to-fruit length.*   The calyx can be well developed but extending only halfway up the fruit, as in *Corylopsis* (fig. 7C) and *Hamamelis* (fig. 7A). In *Sinowilsonia*, the calyx is quite thin but engulfs the entire fruit (fig. 7E); in *Parrotia* it is reported to cover the basal quarter of the fruit.

10. *Shape of the fruit apex.* A prominent ridge sometimes referred to as either a "pointed or acute tip" of the fruit (Zhang et al. 2003) is present on the fruit apex of *Hamamelis*. A somewhat reduced version occurs in *Corylopsis* and *Parrotia*. This character is absent in most of the other genera, including *Fothergilla*, *Distylium*, and *Sinowilsonia*.

11. *Seed morphology.* The seeds of Hamamelidoideae are all relatively ellipsoid and wingless, with a hard and smooth seed coat and distinct hilar scar. Most are of comparable size and morphology (Endress 1993). *Corylopsis* has been described as having a particular variation in the shape of the hilar scar and facet (Grote 1989; Manchester 1994; Zhao et al. 2008).

12. *Seed coat anatomy.* Seed coat anatomy has been described for some genera (Netolitzky 1926; Melikian 1973; Rao 1974; Corner 1976; Manchester 1994; Zhang and Wen 1996; Zhao et al. 2008), but to date there has been no comprehensive survey of the entire subfamily. Interestingly, although external morphology of seeds is generally similar, there is notable variation in seed anatomy where it is known. For the purposes of comparing *Hamawilsonia* to extant genera, we examined the seed coat anatomy of *Sinowilsonia*, *Hamamelis*, *Corylopsis* (fig. 5G–5I), and *Distylium* (table 2).

The seed coats of extant genera of Hamamelidoideae appear to be fairly uniform in their developmental features, but they vary in the details of mature anatomy. Seed coats are derived from a typical double integument, with the layers that are developed from the outer integument termed the "testa" and those from the inner integument called the "tegmen" (Corner 1976). The mature seed coat can be divided into three layers, the exo-, meso-, and endotesta, all derived from the testa, while the tegmen contributes little (Corner 1976; Zhang and Wen 1996). All of the cells in the mature testa are highly sclerified, resulting in a hard seed coat. Remnants of the tegmen typically are crushed (Corner 1976).

Our comparison of seed coat anatomy for selected genera of Hamamelidoideae shows variation in cell sizes, orientations, and number of cell layers (table 2). Overall seed coat thicknesses are quite similar (table 2), and the extotesta of all genera in this group is uniseriate (Zhang and Wen 1996). *Sinowilsonia* and *Distylium* have an exotesta of small, cuboidal cells (20–25 μm high $\times$ 20 μm wide) with darker contents than the rest of the seed coat. In *Corylopsis* and *Hamamelis*, the exotestal layer is composed of larger cells that are cuboid to almost palisade in transverse section (fig. 5G, 5H).

Much of the variation in the seed coat within genera exists in the mesotesta (table 2). The thickest mesotesta of those surveyed is in *Sinowilsonia* (18 cells thick at its widest point; fig. 5I) with an outermost zone approximately six cells thick of radially aligned cells, with few interspersed tangential cells. The inner zone is ~12 cells thick, and cells are markedly tangentially elongate, 20 μm high $\times$ >195 μm wide. In *Distylium* and *Corylopis*, the mesotesta is of similar construction but half as thick (up to nine cells) and composed of larger radially elongate cells two to three cells thick in the outer region to considerably smaller, radially aligned cells six to seven cells thick to the inside (table 2). *Hamamelis* has a distinctive, undifferentiated mesotestal layer 12–13 cells thick, with a pattern of interspersed radially and tangentially aligned cells throughout (fig. 4G). Endotestal cells typically

are tangentially aligned (*Distylium*, *Corylopsis*, and *Hamamelis*) except in *Sinowilsonia*, where cells tend to be radially oriented. The endotesta varies from thinner (two to five cells thick) in *Corylopsis* and *Sinowilsonia* to thicker (eight to 10 cells thick) in *Distylium* and *Hamamelis* (table 2). *Hamawilsonia* possesses a mosaic of features of the seed coat not found within any of the known extant Hamamelidoideae genera. The exotesta is apparently comparable to *Hamamelis* and *Corylopsis* in having large cuboidal cells (fig. 4F–4H). Cells of the mesotesta, which comprises the bulk of the seed coat, are radially elongate and grade from smaller to larger toward the inside. In this regard, the seed coat is most similar to *Corylopsis*. The innermost zone, which is the least preserved of the layers, is similar to most of the genera studied, except for *Sinowilsonia*, in having tangentially elongate cells (table 2).

Evolution and Biogeography of Hamamelidoideae

The Hamamelidoideae most likely appeared in the Cretaceous (Endress and Friis 1991; Magallón 2007). However, like *Hamawilsonia*, Cretaceous floral mesofossils also have combinations of characters representative of all three clades of extant Hammelidoideae (Magallón 2007). The Late Paleocene *Hamawilsonia* shares its infructescence type and some features of seed coat anatomy with both *Corylopsis*, a member of the basal loropetalid clade, and *Sinowilsonia*, a member of the derived eustigmatid clade (fig. 1). Associated pollen catkins and pollen also indicate close affinities with *Sinowilsonia*. *Hamawilsonia* also has similarities with *Hamamelis*, a member of the fothergillid clade, including a similar fruit shape and anatomy and some seed coat similarities.

Given the long history of the Hamamelidoideae, with fossils assignable to the family appearing in the Late Cretaceous and fossils of extant taxa first represented by the Eocene (Radtke et al. 2005), the presence of the mosaic taxon *Hamawilsonia* in the Late Paleocene strongly indicates that Hamamelidoideae experienced a radiation during the Paleocene-Eocene thermal maximum. Fifteen of the 22 extant taxa belonging to the subfamily are found in subtropical-tropical environments, and all of these taxa are derived within the subfamily (fig. 1B).

The Asian–North American disjunct distribution of *Hamamelis* has been investigated (Wen and Shi 1999; Li et al. 2000), and the biogeographical patterns of disjunct distributions of genera in the Northern Hemisphere have been explored (Wen 1999; Donoghue et al. 2001). What is interesting regarding the Hamamelidoideae is the presence of Asian–Central American disjunct distributions in two separate clades—the one containing *Corylopsis* and the one containing *Sinowilsonia* (fig. 1).

Definitive seeds and fossil leaves of *Corylopsis* appear in Europe and eastern and western North America during the Eocene, while fossils assignable to *Matudaea*, a taxon with a current distribution in Mexico and Central America, are reported from the Neogene of Europe (Mai and Walther 1985; Radtke et al. 2005; Magallón 2007). The simplest explanation for this disjunction is that *Matudaea* radiated into Central America via North America. However, no fossil record for *Matudaea* in North America has been found to document this proposed interchange.

The most derived of the three major clades within the Hamamelidoideae, the eustigmatid clade, which contains *Sinowilsonia*, has species distributed among three Southern Hemisphere continents. Two lineages exist within this clade, one that *Sinowilsonia* belongs to, which contains an Asian–Central American disjunction, and a second clade consisting of African and Australian lineages (fig. 1) and including the genera *Trichocladus*, *Dicoryphe*, *Ostrearia*, *Noahdendron*, and *Neostrearia*. The last three of these genera lack a fossil record.

Raven and Axelrod (1974) postulated that the relationship between the Australian genera of Hamamelidoideae and the Madagascan *Dicoryphe* were recent arrivals from Asia during the Miocene and that the existence of *Dicoryphe* in Madagascar might reflect Paleocene or earlier migration of Hamamelidaceae-Hamamelidoideae to Africa from Laurasia. Alternatively, they suggested that the group may have differentiated in West Gondwanaland.

The derived position of the Australian and African-Madagascar taxa within the phylogeny strongly indicates that these taxa did not differentiate within Western Gondwana but probably represent dispersal events into Africa and Australia from Europe or Asia. There is documentation of Laurasian elements being present past the K-T (Cretaceous-Tertiary) boundary in Africa from both Tunisia and West Africa, including Juglandaceae (Jacobs 2004). Based on the Eocene appearance of fossils assignable with some confidence to extant genera within Hamamelidoideae (Radtke et al. 2005) and the mosaic nature of the Paleocene form described herein, a working hypothesis is that the African-Madagascar taxa represent a lineage that may have dispersed into Africa during the Late Cretaceous or Paleocene and evolved in East Africa and Madagascar. However, additional micro- and megafossil evidence is sorely needed, as well as analytical biogeographical tests of this hypothesis using data from other groups that are disjunct between Asia and Africa. There is a biogeographical bias of studying exclusively Northern Hemisphere (Wen 1999; Donoghue et al. 2001; Donoghue and Smith 2004) or Southern Hemisphere disjunctions (Sanmartin and Ronquist 2004), but exploring the biogeographical relationships among disjunctions between the north and south, particularly between Eurasia and Africa, requires explanations other than the standard vicariance models that have dominated Southern Hemisphere biogeographical studies.

Acknowledgments

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