

# *Fagus* (Fagaceae) fruits, foliage, and pollen from the Middle Eocene of Pacific Northwestern North America

Steven R. Manchester and Richard M. Dillhoff

**Abstract:** Fruits and leaves from the Middle Eocene of McAbee, British Columbia, and Republic, Washington, provide an earlier record for the genus *Fagus* than previously accepted for this member of the Fagaceae. The fruits are trigonal nuts borne within spiny four-valved cupules on long peduncles. The leaves are borne alternately on the twigs and are ovate to elliptic with craspedodromous secondary veins and simple teeth distributed one per secondary vein. The shale preserving these megafossils also contains dispersed pollen with morphology and ornamentation diagnostic of *Fagus*. Previously, the oldest *Fagus* occurrences confirmed by fruits were early Oligocene (ca. 32 Ma). The recognition of Middle Eocene (ca. 50 Ma) representatives helps to reduce the disparity between molecular evidence favoring *Fagus* as a primitive genus within Fagaceae, and fossil evidence, which had indicated older occurrences of *Castanea* and *Quercus* than *Fagus*.

**Key words:** Eocene, *Fagus*, fossil, foliage, fruits, British Columbia.

**Résumé :** Des fruits et des feuilles de l'Éocène moyen provenant de McAbee en Colombie-Britannique, et de Republic dans l'État de Washington, constituent une mention antérieure pour le genre *Fagus*, par rapport à ce qui est généralement accepté pour cette entité des Fagaceae. Les fruits sont des noix à trois côtés, développées dans des cupules à quatre valves portées sur de longs pédoncules. Les feuilles se forment en alternance sur les rameaux; ils sont ovés à elliptiques avec des veines secondaires craspedodromes et des dents distribuées à raison d'une par veine secondaire. Le schiste préservant ces méga-fossiles contient également des pollens dispersés, avec une morphologie et une ornementation caractéristiques des *Fagus*. Auparavant, la mention la plus ancienne des *Fagus*, confirmée par des fruits, provenait du début de l'Oligocène (ca 32 Ma). La reconnaissance de représentants de l'Éocène moyen (ca 50 Ma) aide à réduire la disparité entre les preuves moléculaires favorisant les *Fagus* comme genre primitif des Fagaceae, avec les preuves fossiles, qui indiquait une préséance des *Castanea* et des *Quercus*, par rapport aux *Fagus*.

**Mots clés :** Éocène, *Fagus*, fossile, feuillage, fruits, Colombie-Britannique.

[Traduit par la Rédaction]

## Introduction

Beech trees have an extensive fossil record in the Northern Hemisphere based on foliage and fruits of the genus *Fagus*. The fossil occurrences have been reviewed in systematic treatments of this genus in the European (Kvaček and Walther 1991a, 1991b; Denk and Meller 2001) and Asian (Tanai 1974, 1995; Iljinskaya 1982; Liu et al. 1996; Uemura 1980) Tertiary.

*Fagus pacifica* Chaney from the early Oligocene Bridge Creek flora of Oregon (Chaney 1927; Meyer and Manchester 1997; Denk and Meller 2001) has been regarded as the oldest occurrence of this genus based on both fruits and leaves. However, the Oligocene age of about 32 Ma indicated for the Bridge Creek flora postdates by more than 22 million

years the earliest fruit records of other extant genera including *Castanea* (Middle Eocene of Tennessee; Crepet and Daghlion 1980; personal observations) and both *Castanopsis* and *Quercus* (Middle Eocene of Oregon; Manchester 1994). The relatively late occurrence of *Fagus* compared with other extant and fossil genera of the family seemed paradoxical in view of molecular data suggesting a basal divergence of *Fagus* from other Fagaceae species (Manos et al. 2001; Li et al. 2004). Cupules of *Fagus* are similar in appearance to those of the Southern Hemisphere genus *Nothofagus*, which formerly was also included in the Fagaceae; however, that genus differs substantially from *Fagus* and other genera of the family in pollen morphology, leaf architecture, and chromosome number, supporting its recognition as a separate family, Nothofagaceae (Nixon 1989).

Leaves resembling *Fagus* were previously recognized from the Middle Eocene of Republic Washington, One Mile Creek, British Columbia (Gandolfo 1996), and sites in China (Liu et al. 1996), but until recently, the lack of convincing reproductive structures caused us to regard the identification of the leaves as *Fagus* as tentative. Recently, the fossil record of *Fagus* has been extended back to the Middle Eocene based on cupule and nut impressions mentioned and figured

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**S.R. Manchester**,<sup>1</sup> Florida Museum of Natural History, Gainesville, FL 32611, USA.

**R.M. Dillhoff**, Evolving Earth Foundation, P.O. Box 2090, Issaquah, WA 98027, USA.

<sup>1</sup>Corresponding author (e-mail: [steven@flmnh.ufl.edu](mailto:steven@flmnh.ufl.edu)).

by Pigg and Wehr (2002) from the Middle Eocene of Washington, USA, and British Columbia, Canada. In the present paper, we formally describe this new species, based on co-occurring reproductive organs and leaves from the Middle Eocene lacustrine shales of McAbee, western British Columbia.

## Materials and methods

This investigation was based on specimens from three localities of similar Middle Eocene age. Most of the specimens of leaves and fruits were collected from the McAbee locality, situated at N50°47.818' W121°08.568' near the town of Cache Creek, British Columbia. Additional leaves (e.g., Gandolfo 1996, Fig. 5) and a few nuts (e.g., Pigg and Wehr 2002, Fig. 15) were observed in collections from Republic, Washington. Rare leaves of the same kind were also observed from the One Mile Creek site, near Princeton, British Columbia (e.g., Gandolfo 1996, Fig. 6). This analysis was based primarily on specimens deposited at the Burke Museum (UWBM), Seattle, Washington, University College of the Cariboo, Kamloops, British Columbia, Canada (UCC), and the Florida Museum of Natural History (UF), Gainesville, Florida.

To determine whether *Fagus* pollen was deposited along with the fruit and leaf remains, a small piece of shale bearing a *Fagus* leaf impression from McAbee was crushed and processed for dispersed pollen. The sample was digested in hydrofluoric acid and then washed in water. The organic residue was extracted using heavy liquid (a saturated solution of ZnCl<sub>2</sub>). The resulting residue contains cuticle fragments as well as pollen and spores. Attempts at further processing (such as the standard treatment in Schultze's solution followed by KOH) resulted in selective destruction of the more fragile palynomorphs including *Fagus*. Therefore, the un-macerated residue was simply washed in water and mounted for study by light and scanning electron microscopy (SEM). A drop of the residue was evaporated onto a circular glass coverslip, which was temporarily mounted face-up on an aluminum stub for SEM. After locating and imaging *Fagus* grains by SEM, the coverslip was removed from the stub, and mounted face-down with a drop of glycerine jelly on a glass microscope slide for light microscopy of the same pollen grains.

## Systematics

Family        Fagaceae  
Genus        *Fagus* L.  
Species      *Fagus langevinii*

## Species description

*Fagus langevinii* sp. n. Figs. 1–4

HOLOTYPE: UWBM 97583, a cupule (Fig. 1A).

PARATYPES: UWBM 7433, 97584–97589, UCC F349 (cupules), UWBM 97603, 97590, 97591 (nuts), UWBM 97598 (twig bearing leaves), UWBM 97592–97597, 97599–97602, UF 26087, 42584, 42585 (leaves).

ETYMOLOGY: This species is named to honor David Langevin whose love of the McAbee site has led to the discovery and conservation of numerous important fossil specimens.

DIAGNOSIS: Pedunculate cupules. Cupule ovate, composed of four ovate valves fully enclosing two trigonal nuts. External surface with spiny appendages occasionally bifurcate near tip. Peduncle long (up to 2.5 times as long as the cupule), thickened near junction with cupule. Nuts triangular in cross section, ovate, elliptical, to obovate in face view, with a narrow wing or flange developed along the three angles of the nut. Sepals arising from apex of nut and surrounding the three styles.

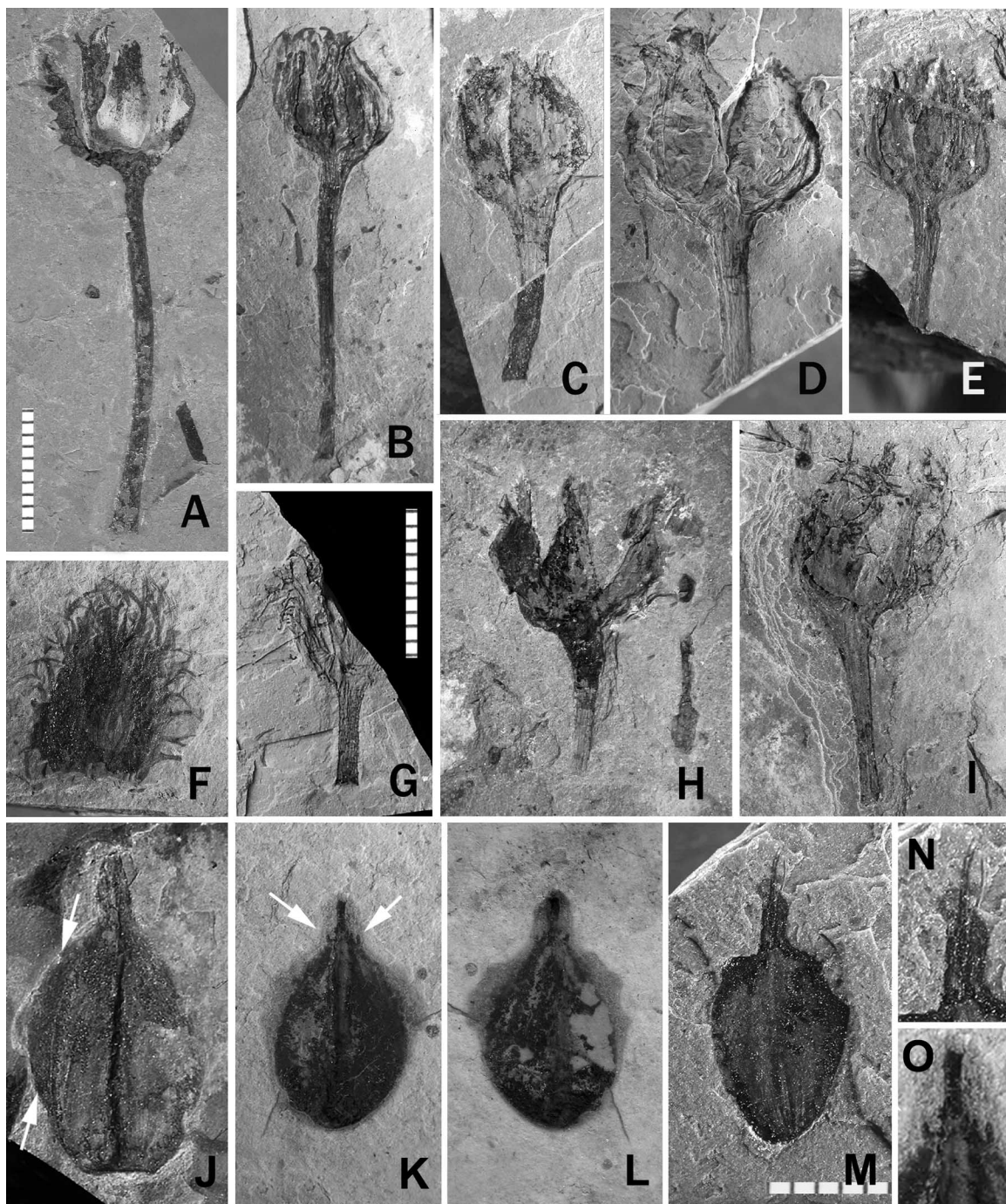
DESCRIPTION: Cupule (Figs. 1A–1I) ovate, 10–14 mm in length and 8–13 mm wide, composed of four ovate valves, fully enclosing two trigonal nuts. Appendages spiny, up to 1.2 mm long, and occasionally bifurcate near tip (Fig. 1F), often lacking basally (by abrasion). Peduncle long (up to 2.5 times the cupule length), up to 29 mm long and 1.9 mm thick, thickened near junction with base of cupule (Fig. 1C). Nuts (Figs. 1J–1M) triangular in cross section, ovate, elliptical, to obovate in face view, length 7.0–10.5 mm, width 4.5–7.5 mm, a thin wing or flange developed along the three angles of the nut (or apparently absent; see discussion). Sepals up to 1.3 mm long, arising from apex of nut and surrounding the three styles, which are 1.3–2.5 mm long (Fig. 1M).

Leaves alternate, subtending enlarged, rounded, non-stipitate, axillary buds. Petiole slender (0.8–1 mm thick), 7–13 mm long. Lamina ovate to elliptic, 52–193 mm long, 27–74 mm wide, average L:W ratio 2.1:1, symmetrical (Figs. 2B–2D) to asymmetrical (Figs. 2A, 2F, and 4B) at the base; basal angle acute (Fig. 2C) to rarely obtuse (Fig. 2D), basal flanks typically convex, occasionally cuneate or decurrent; apex angle acute, with typically convex flanks. Margin serrate (Figs. 2A and 2B) to subtly crenate (Figs. 2C, 3A, and 3B). Venation pinnate, craspedodromous. Primary vein moderately thick, straight, not sinuous. Secondary veins 9–17 pairs, (mean 11), arising decurrently from the primary at angles of 40–60° (decreasing apically), markedly parallel and uniform, straight to slightly concave. Intersecondaries, agrophic and fimbrial veins absent. Tertiary veins percurrent, mostly opposite, occasionally alternate, straight to sinuous, spaced 1.4–3.5 mm apart (3 to 7 per cm) at angles of 135–150° near base and 105–130° apically; increasing basally. Quaternary veins alternate percurrent to regular polygonal reticulate, 4th and 5th order veins forming an orthogonal reticulum, areolation well developed (Fig. 3E) consisting of 4- to 5-sided polygons averaging 0.2 mm, freely ending veinlets straight to curved, once branched. Teeth simple, regularly spaced, one per secondary vein, nonglandular, basal flank convex/straight, apical flanks concave/straight, sinuses rounded.

Associated dispersed pollen tricolporate, prolate to spheroidal, rounded in polar view. Polar axis width 16–20 µm, equatorial diameter 19–30 µm. Colpi long and narrow, extending about 90% of the distance from the equator toward each pole. Surface appearing psilate to finely verrucate by light microscopy (Fig. 4A), but with vermiform woven microornamentation with freely ending rod-like elements observable by SEM (Figs. 4B–4D).

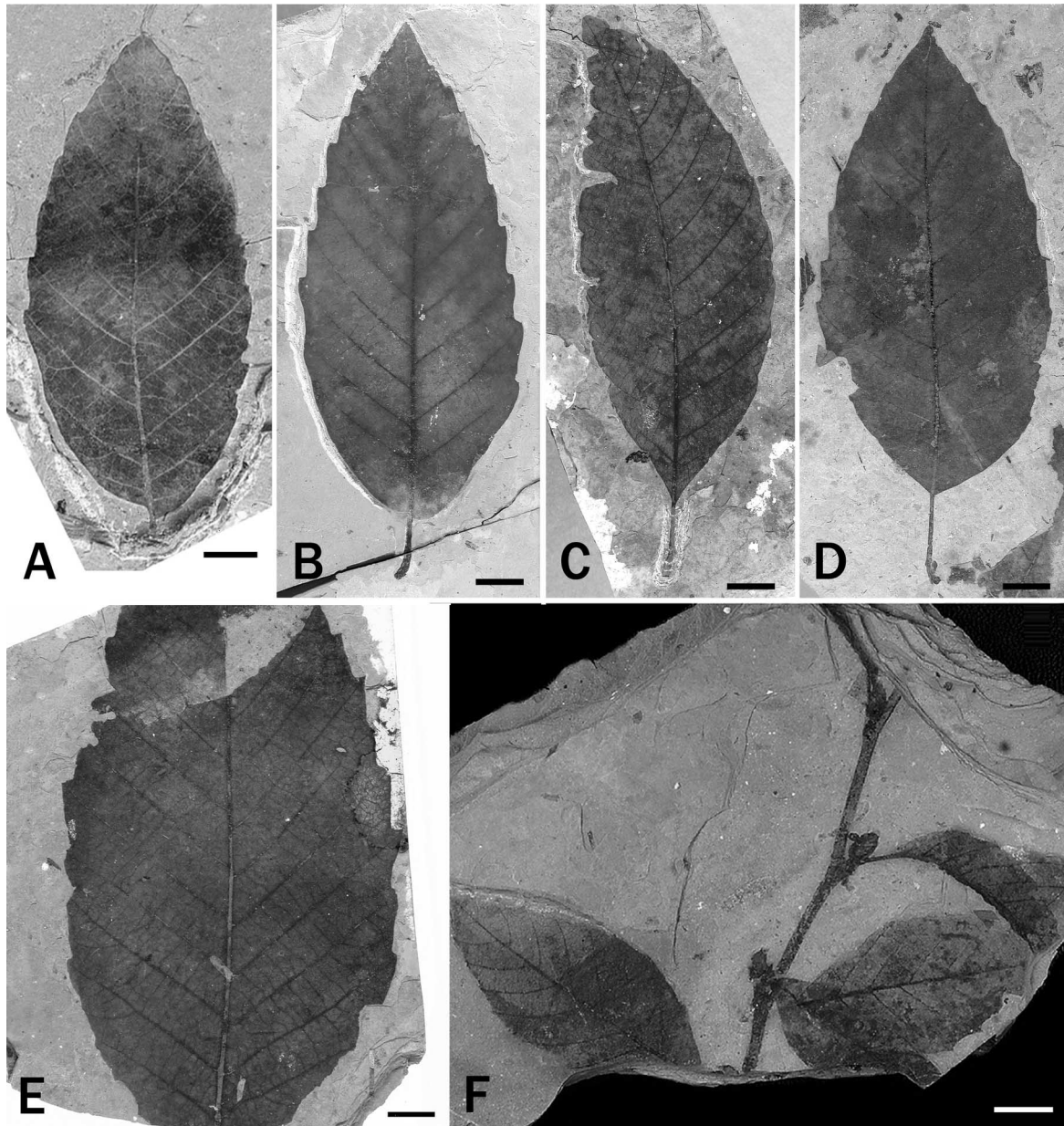


**Fig. 1.** Fruits of *Fagus langevinii* sp. nov. (A–I) Cupules. (A) Holotype, showing long peduncle and four valves with abaxial spiny ornamentation, UWBM 97583. (B) Specimen with long peduncle and ovate cupule with spines preserved near the apex of the valves, UWBM 97584. (C) Specimen showing the cleft between two adjacent valves, UWBM 97585. (D) Cupule showing two prominent bulges, presumably representing the position of two nuts, UCC F-349. (E) Another cupule showing spiny projections preserved apically, UWBM 97586. (F) A single detached cupule valve showing well preserved spines, some of the which have bifurcate apices, UWBM 97587. (G) Cupule with short (broken?) peduncle, and spiny valves, UWBM 7433. (H) Cupule with spread valves, UWBM 97588. (I) UWBM 97589. (J–O) Beech nuts. (J) Nut showing truncate base, medial keel, and apically protruding perianth. Note also the lateral wing preserved on left side (arrows), UWBM 97603. (K) Smaller ovate nut showing apical style and sepals (arrows), a median keel representing the junction of two lateral faces, UWBM 97590A. (L) Counterpart of the specimen in K. Note that this face lacks a median keel, because it represents a single flat face of the trigonal nut. (M) obovate nut with three styles protruding beyond the apical sepals, UWBM 97591. (N) Detail of styles from Fig. 1M. (O) Detail of perianth and style from Fig. 1K. Scale bars are calibrated in millimeters; scale bar = 10 mm in Fig. 1A and also applies to Figs. 1B–1F, 1H, and 1I; scale bar = 5 mm in Fig. 1M and also applies to Figs. 1J–1L.





**Fig. 2.** Leaves of *Fagus langevinii* sp. nov. (A) Elliptical lamina with asymmetrical base, UWBM 97592. (B) Leaf with short petiole and markedly toothed lamina, UWBM 97593. (C) Leaf with damaged left margin and subtly crenate right margin, UWBM 97594. (D) Leaf with complete slender petiole, serrate lamina with obtuse base and acute apex, UWBM 97595. (E) Larger lamina showing well preserved, closely spaced percurrent tertiary veins, UF18437-42584. (F) Twig bearing three leaves and prominent nonstipitate axillary buds, UWBM 97598. Scale bars = 1 cm.



## Discussion

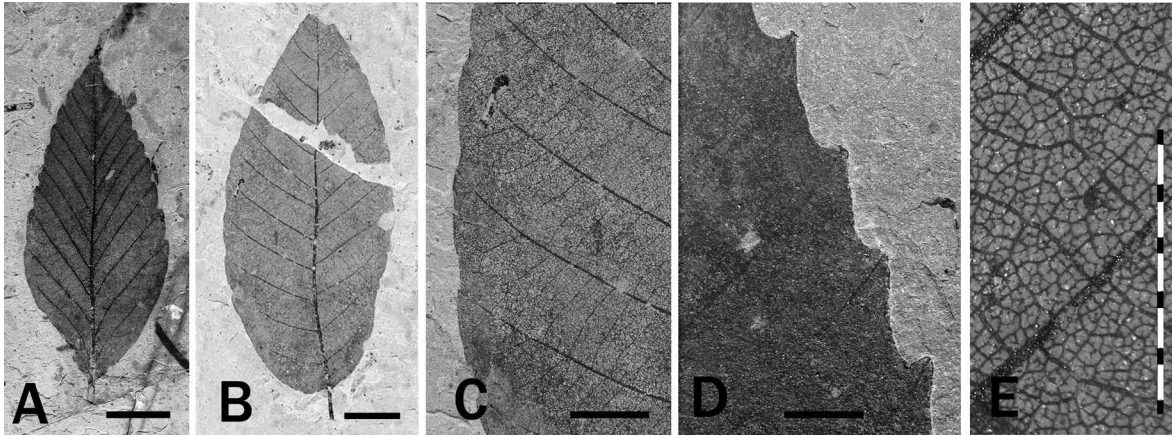
For the establishment of this new species, we have designated one of the cupule specimens as the holotype (Fig. 1A). Hence the name is formally based on the reproductive structures as indicated in the diagnosis rather than the isolated foliage or pollen. However, the associated foliage and pollen conform morphologically to *Fagus*, and there is no indication of more than one species of the genus at McAbee, so we hypothesize that these organs represent the same species, which in life may have borne twigs similar to that recon-

structed in Fig. 5. The description above is based exclusively on specimens from the type locality, but we have observed similar nuts (Pigg and Wehr 2002) and foliage (Gandolfo 1996) from Republic, Washington.

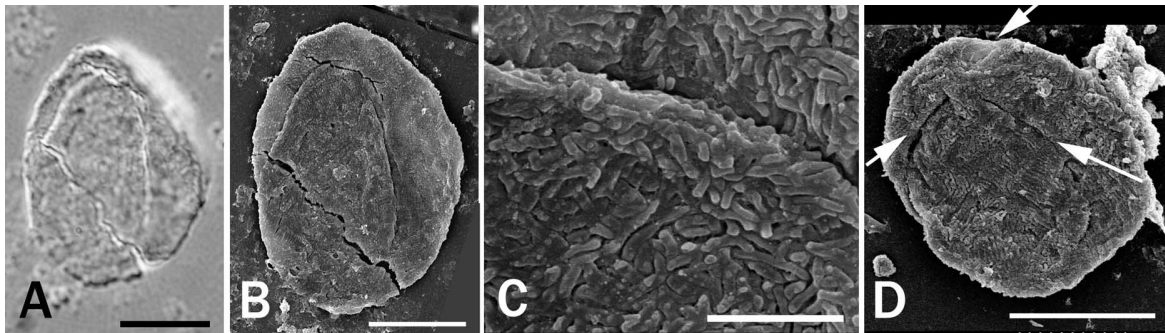
The affinities of both fruits and foliage to *Fagus* are clear. Spiny four-valved cupules completely enclosing two trigonal nuts are diagnostic of *Fagus*. Trigonal nutlets and valvate involucre also occur in the trigonobalanoid genera, *Trigonobalanus*, *Colombobalanus*, and *Formanodendron* (nicely illustrated by Nixon and Crepet 1989), but in these genera the cupules do not completely cover the apex of the



**Fig. 3.** Leaves of *Fagus langevinii* sp. nov. (A) Smaller lamina than those in Fig. 2, with crenate margin, UWBM 97599. (B) Lamina with subtly crenate margin, UWBM 97600. (C) Detail from Fig. 3B, showing secondary veins craspedodromous to the marginal crenations. (D) Detail of margin showing sharp to rounded teeth, rounded sinuses, and craspedodromous secondary veins, UWBM 97601. (E) Well-preserved higher order venation, UWBM 97602. Scale bars = 10 mm in Figs. 3A, 3B, and 3D; scale bar = 5 mm in Figs. 3C and 3E.



**Fig. 4.** Dispersed pollen of *Fagus* from the same shale as the fruits and leaves of *Fagus langevinii*. (A) A grain in nearly equatorial view showing apparently finely verrucate surface, light microscopy. (B) The same pollen grain, viewed by SEM. (C). Detail of vermiform microornamentation enlarged from the same grain as Figs. 4A and 4B. (D). Subpolar view showing rounded outline, and three colpi (arrows) that reach closely to the pole. Scale bars = 10  $\mu$ m in Figs. 4A, 4B, and 4D; scale bar = 2  $\mu$ m in Fig. 4C.



nuts, there is a variable number of nuts per cupule (most commonly) and the arrangement of scales on the cupule is different.

Foliar features that the fossil species shares with extant *Fagus* include the short petioles, the laminae with evenly spaced, parallel secondary veins and closely spaced percurrent tertiary veins, the lack of intersecondary and pectinal veins, and the serrate margin with nonglandular teeth arranged one per secondary vein. Similar leaves in other fagaceous genera can be distinguished by attention to additional details of venation. The absence of spines on the teeth and lack of a marginal vein, distinguishes the fossil from *Quercus*. Similar leaves of *Colombobalanus* are distinguished by having teeth confined to the upper two-thirds of the lamina.

*Fagus langevinii* fruits are known from isolated cupules (Figs. 1A–1I), some of which retain nut(s), and by isolated nuts (Figs. 1J–1M). The trigonal shape of the nutlets can be inferred from the way that they are compressed in the shale. When the shale containing a single nut is cleaved apart, both halves show the same ovate outline of the compressed nut,

but one side shows an uninterrupted smooth surface (Fig. 1L), while the counterpart shows a prominent median crease (Fig. 1K), representing the keel formed by the two additional faces of the trigonal nut. Although none of the specimens clearly shows both nuts intact within the cupule (likely they had already shed their nuts), some specimens show two bulges interpreted to reflect the former position of the nuts (Fig. 1D).

It appears probable that most of the nuts and cupules suffered abrasion and (or) deterioration prior to being deposited in the lake sediments of McAbee. The cupules show the spines clearly toward the apex (Figs. 1B–1E), but those along the main body of the cupule vary from being short to absent, except in the holotype (Fig. 1A) and in one isolated cupule valve in which the spines are clear with bifurcate tips (Fig. 1F). Denk and Meller (2001) documented various stages of abrasion in extant *Fagus* cupules, and it seems likely that these fossils are secondarily denuded of some of the spines. Similarly, the wings of the nut are not clearly visible on some specimens (Figs. 1K–1M), but one specimen (Fig. 1J) clearly shows a wing flanging one of its lateral

**Fig. 5.** Reconstruction of *Fagus langevinii* as it may have appeared in life. Diagram by Johan Gerhard Marx.



margins. Perhaps the wings were variable in their presence or absence as in some modern species (Denk and Meller 2001), or these thin flanges may have been lost to abrasion or rotting. One of the specimens shows a faint halo of mineralization surrounding the nut in the position where the wing might have been (Fig. 1L). The wing is considered to be an important feature separating different species of *Fagus*, but in fossils the loss by abrasion must also be considered (Denk 2003).

Dispersed pollen grains matching those of *Fagus* were common in the shale along with the leaves. By light microscopy, the grains are tricolporate and apparently psilate (Fig. 4A). Without additional information from SEM, these might be interpreted as belonging to other fagaceous genera, or even to some other genera of dicotyledons. However, microornamentation of the grains as revealed by SEM was found to be distinctive: vermiform, woven with freely ending rod like elements (Figs. 4B–4D). Among extant and extinct genera so far known from the Fagaceae, this pattern is apparently restricted to *Fagus*. Although vermiform woven microsculpture occurs in some Castanoideae as well as in *Fagus* (Crepet 1989), the presence of frequent freely ending rod-like elements seems to be confined to *Fagus* (Crepet and Daghljan 1980; Pragłowski 1982; Walther and Zetter 1993; Denk 2003). Few other studies have attempted to link dispersed fagaceous pollen with the fossil leaves of the same biological entity with the use of both light and electron microscopy. The best example is that of Walther and Zetter (1993), who found clumps of fagaceous pollen adhering to fossil leaf cuticles, allowing them to infer the morphologically distinct pollen types produced by leaves identified as *Eotrigonobalanus*, *Trigonobalanopsis*, *Lithocarpus*, and *Fagus*.

#### Comparison with extant species.

*Fagus* was divided into two subgenera in an unpublished dissertation (Shen 1992); and these two groups merit recognition on morphological grounds (Denk 2003), but the names for them have not yet been validly published. Based on features of foliage and cupules of extant species, Zetter

(1984) and Kvaček and Walther (1991a, 1991b) recognized four groups within the genus. These are partially consistent with a phylogenetic analysis of nine extant species of *Fagus* (Manos and Stanford 2001), based on ITS and cpDNA. Nucleotide variation was relatively low, giving only 24 informative characters. Designating *Trigonobalanus verticillata* as an outgroup, they found a single, well-supported, most parsimonious tree. The results are difficult to compare meaningfully with the morphological groups recognized by Zetter (1984) and Kvaček and Walther (1991a, 1991b), because fewer species were included and the two accessions attributed to *F. crenata* came to different positions in the resulting tree, suggesting that one of the accessions was misidentified, or that *F. crenata*, as currently circumscribed, is polyphyletic. A separate ITS study by Denk et al. (2002) included several samples per species and revealed excessive intraspecific and intragenomic ITS variability in the genus, giving limited phylogenetic resolution and causing the authors to question the topologies of Manos and Stanford (2001). Additional morphological characters were included in another analysis of modern and fossil species by Denk (2003). The four morphological groups of Zetter (1984) and Kvaček and Walther (1991a, 1991b) (Table 1) are summarized below, augmented by observations from Denk (2003):

The first group includes the Asian species *Fagus engleriana* Seemen, *Fagus multinervis* Nakai (apparently a synonym of *F. engleriana*; Denk 2003), *Fagus japonica* Maxim., and, according to Kvaček and Walther (1991a, 1991b) *Fagus longipetiolata* Seemen. These species have cupules with extremely long peduncles that are about three times longer than the cupule, and leaves that are strongly papillate beneath, with anomocytic stomata. *Fagus longipetiolata* was excluded from this group by Zetter (1984) and Denk (2003), but it conforms in that it has papillate lower epidermis and anomocytic stomata. Denk (2003) observed that wax ornamentation was also present on the lower epidermis in all these species but absent in other *Fagus* species. The species of this group have pollen with long colpi that reach at least 90% of the distance from the equator toward each pole (Pragłowski 1982; Denk 2003). Collections attrib-



**Table 1.** Comparison of *Fagus langevinii* with extant groups of *Fagus*, emphasizing selected characters from Pragłowski (1982), Zetter (1984), Kvaček and Walther (1991a, 1991b), and Denk (2003).

	Peduncle length	Buds	Secondary venation	Stomata	Leaf lower surface	Pollen colpi
<b>Group 1</b> <i>F. engleriana</i> <i>F. multinervis</i> <i>F. engleriana</i> <i>F. japonica</i>	3× cupule length	Stipitate	Craspedodromous	Anomocytic	Papillate	Long
<b>Group 1a*</b> <i>F. longipetiolata</i>	Up to 3× cupule length	Sessile	Craspedodromous	Anomocytic	Papillate	Variable short and long
<b>Group 2</b> <i>F. hayatae</i> <i>F. lucida</i> <i>F. panshanica</i> <i>F. chienii</i>	Up to 2× cupule length	Sessile	Craspedodromous	Cyclocytic	Nonpapillate	Short (some subspecies not checked)
<b>Group 3</b> <i>F. grandifolia</i>	Less than 1× cupule length	Sessile	Craspedodromous	Small anomocytic	Nonpapillate	Long
<b>Group 4</b> <i>F. crenata</i> <i>F. orientalis</i> <i>F. sylvatica</i>	Up to 2× cupule length	Sessile	Pseudocraspedodromous or eucamptodromous	Actinocytic, cyclocytic	Nonpapillate	Short
<b><i>F. langevinii</i></b>	Up to 2.5× cupule length	Sessile	Craspedodromous	?	?	Long

\*The position of *F. longipetiolata*, whether in group 1 or group 2, has been a matter of disagreement among Pragłowski (1982), Zetter (1984), Kvaček and Walther (1991a, 1991b), and it is treated separately for this comparison.

uted to *F. longipetiolata* seem to be more variable, sometimes having shorter fruit peduncles, and with pollen varying from long to short colpi (Denk 2003). Three species of group 1, *F. engleriana*, *F. multinervis*, and *F. japonica*, were distinguished from other extant species by densely spaced percurrent tertiaries (9–13 per cm; Chelebaeva 1980; Zetter 1984); however, this character should be viewed with caution because Denk (2003) found that shade leaves in all species may have significantly more widely spaced tertiary veins than sun leaves on the same tree. According to Denk (2003), *F. engleriana* and *F. japonica* have stipitate buds, whereas *F. longipetiolata* and all other species have sessile buds.

The second group includes the southern east Asian species *Fagus hayatae* Palib. ex Hayata, *Fagus lucida* Rehder. et Wilson, *Fagus panshanica* Yang, and *Fagus chienii* Ching. It has fruits with short peduncles, (equal to or up to twice the length of cupule). The leaves are not papillate beneath and have cyclocytic stomata. The pollen colpi are short in *F. hayatae*, but pollen morphology is unknown for the other species.

The third group includes the North American species *Fagus grandifolia* Ehrh. and segregate species *Fagus mexicana* Martinez. These have cupules on short peduncles (less than or equal to the cupule length) and nonpapillate leaves with distinct teeth, craspedodromous secondary venation, and small anomocytic stomata. Pollen colpi are narrow and long as in group one (Pragłowski 1982; Denk 2003)

The fourth group, including *Fagus crenata* Blume, *Fagus orientalis* Lipsky, and *Fagus sylvatica* L., has mostly entire-margined leaves, pseudocraspedodromous or eucamptodromous venation in which the secondary veins bend upward at the margin rather than entering into teeth. Rather than teeth, some leaves have a slight indentation of the mar-

gin corresponding to the position of each secondary vein. The lower epidermis lacks papillae and has large stomata with actinocytic arrangement (except *F. orientalis* which is partly cyclocytic). *Fagus crenata* and *F. orientalis* have spatulate processes as well as spines on the cupules. The cupule peduncles are short to moderately long. In the molecular sequence study, *F. orientalis* and *F. sylvatica* are resolved as sisters to each other. Pollen of these species have short colpi (extending only about 50% of the distance from equator toward each pole).

Compared with the four groups of modern species discussed above, *Fagus langevinii* is most readily distinguished from group 4 because of differences in cupule spine morphology (not spatulate), length of the pollen colpi (long in the fossil; short in group four species), secondary venation (craspedodromous in the fossil, pseudocraspedodromous in group four species) and the leaf margin (serrate in the fossil, indented in group four species). The long colpi of the fossil pollen (Figs. 4B and 4D) indicate that *F. langevinii* is similar to groups 1 and 3 and not to groups 2 and 4 (Table 1).

A twig of *F. langevinii* with intact axillary buds (Fig. 2F) shows that the buds were sessile, as in most extant species of *Fagus*. This contrasts with the conspicuously stipitate buds found in group 1 species, such as *F. engleriana* and *F. japonica* (Denk 2003). If this character is emphasized, along with the features mentioned above, then our fossil seems to have most in common with group 3, that is, the extant new world taxon *F. grandifolia* (including *F. mexicana*), although the peduncles in the fossil, which we interpret to range from long (more than twice the length of the cupule; Fig. 1A) to moderately long (about equal to the length of the cupule, Fig. 1I), are longer than is typical in group 3 (Table 1).

Unfortunately, we do not know if the leaves were papillate on their lower surface as in the group 1 species. If the leaves

were nonpapillate, then closer similarity to groups 2 and 3 would be indicated. Denk and Meller (2001) and Denk (2003) cautioned that there is more intraspecific variability in some of the morphological characters than is suggested by previous investigations. For example, they found great variation in cupule peduncle length in *F. silvatica* (10–75 mm) and in *F. engleriana* and *F. japonica* (25–70 mm). Peduncle length variation is also apparent among the peduncles of *F. langevinii* (Fig. 1). In addition, the leaves vary from asymmetrical to symmetrical. In some specimens, the leaf margin is serrate with well-developed, pointed teeth, yet in other instances the margin is only weakly crenate (Fig. 3).

### Other Paleogene *Fagus* occurrences

Wolfe (1977) transferred the species *Tetracera oregona* Chaney and Sanborn (1933) to *Fagus oregona* (Chaney and Sanborn) Wolfe based on leaves from the Late Eocene Goshen flora of western Oregon. It is noteworthy that the number of secondary veins (15–21) is unusually high for *Fagus* (the number observed among extant species usually does not exceed 15; Zetter 1984) and the petiole length, 3.5 cm for a leaf with lamina 14.5 cm long, exceeds that which would be normal in modern species of *Fagus*. The leaves are more similar to those of the genus *Ticodendron* (S. Renner, personal communication, 2003) and, in the absence of associated fruits, the assignment to *Fagus* remains equivocal.

*Fagus pacifica* from the early Oligocene Bridge Creek flora of Oregon (Chaney 1927; Meyer and Manchester 1997) is the oldest previously accepted representative of the genus based on cupules and nuts as well as leaves. *Fagus langevinii* is separated from *Fagus pacifica* by several characters. Nuts of *F. pacifica* are elongate and display more conspicuous wings along the length of the three lateral edges. The peduncle of *F. pacifica* cupules reaches a maximum length of 20 mm with simple spiny appendages. The appendages of *F. langevinii* occasionally bifurcate near the tips and peduncles can be up to 29 mm in length. Laminae of *F. pacifica* from several Bridge Creek localities on deposit in the Florida Museum of Natural History collection range from 47–83 mm in length while those of *F. langevinii* commonly exceed 100 mm, with a recorded maximum of 193 mm, nearly twice the length of the largest known *F. pacifica*. The margin of *F. pacifica* is typically serrate with each tooth coming to a sharp point while those of *F. langevinii* vary from serrate to crenate, with more rounded teeth or crenations. Secondary veins of *F. pacifica* more often are pronouncedly alternate, occasionally resulting in a sinuosity of the primary vein while secondaries are more typically opposite with a straight primary vein in *F. langevinii*. *Fagus pacifica* leaves have a modal average of 12 pairs of secondaries while *F. langevinii* has a mode of only 10 pairs.

Tanai (1995) described a new species of foliage, *Fagus uemurae* from the Early Oligocene Wakamatsuzawa Formation of Kitama City, Hokkaido, Japan. He stated that the singly serrate leaves with minute, obtuse teeth are referable to *Fagus* based on the midvein being sinuate in the upper part of the blade, secondary veins nearly straight to the margin, upturning at the teeth, and the most abmedial tertiary vein from the secondary vein running parallel to the other inter-

costal tertiary veins. He stated that it was similar to other Tertiary species, including *Fagus evenensis* from the Miocene of Kamchatka (Chelebaeva 1980) and *F. pacifica* Chaney. No fruits of *Fagus* were recovered in association with *F. uemurae*.

### Conclusions

Although there are well-substantiated records of the family Fagaceae in the Late Cretaceous based on flowers and fruits (Herendeen et al. 1995; Sims et al. 1998) and secondary xylem (Wheeler et al. 1987), reports recognizing extant genera such as *Quercus* in the Cretaceous (Lesquereux 1874) and Paleocene (Brown 1962) are based mainly on isolated, poorly preserved leaf remains of uncertain affinities. It is possible that extant fagaceous genera did not evolve until the early Tertiary. Additional evidence for the existence of this genus in the Eocene comes from rare leaves in the Fushun and Yilan floras of Northeastern China (*Fagus chinensis* Li; Writing Group of Cenozoic Plants of China 1978; Manchester, personal observation).

The fossil cupules, nuts, leaves, and pollen from McAbee each exhibit characters consistent with the extant genus *Fagus*, indicating that this genus can be safely recognized by the Middle Eocene. The fossil record is compatible with the hypothesis that the genus evolved either in Asia or North America and then spread across Beringia to the other continent. An Asian origin and subsequent dispersals to North America and to Europe, inferred based on phylogeny of extant species, is reasonable (Manos and Stanford 2001). The fossil data do not resolve whether the origin is North American or Asian, but seem to indicate that the arrival to Europe was much later. *Fagus* fruits and foliage are lacking from the many Eocene deposits of Europe, making their first appearance in the Oligocene (Kvaček and Walther 1991a, 1991b). It is noteworthy that the fossil fruits and anatomically preserved leaf remains of the European Tertiary (Kvaček and Walther 1991a, 1991b; Denk and Meller 2001) are similar to the extant North American species and to some of the Asian species, for example, *F. hayatae*, but very distinct from the extant European species, *F. sylvatica*. Apparently the lineage of fossil *Fagus saxonica* in Europe became extinct in Europe during Plio-Pliocene, and its range was reoccupied by the late immigration of *F. silvatica*, which is closely similar to the Asian *F. orientalis*.

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