CORYLUS, CARPINUS, AND PALAEOCARPINUS (BETULACEAE) FROM THE MIDDLE EOCENE KLONDIKE MOUNTAIN AND ALLENBY FORMATIONS OF NORTHWESTERN NORTH AMERICA

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Coryloid reproductive remains (Betulaceae, subfamily Coryloideae) are documented from the middle Eocene Republic flora of northeastern Washington State and the Princeton flora of southern British Columbia. The oldest confirmed examples of two modern genera, Corylus johnsonii Pigg, Manchester & Wehr sp. nov., and Carpinus perryae Pigg, Manchester & Wehr sp. nov., are reported from the Republic flora, and three new species of the extinct genus Palaeocarpinus, Palaeocarpinus barksdaleae Pigg, Manchester & Wehr sp. nov., Palaeocarpinus stonebergiae Pigg, Manchester & Wehr sp. nov., and Palaeocarpinus dentatus (Penhallow) Pigg, Manchester & Wehr comb. nov., are described from Republic, Washington; Princeton, British Columbia; and Stump Lake, British Columbia, respectively. Corylus johnsonii resembles three extant Asian species: Corylus wangii, Carpinus ferox, and Corylus heterophylla. Involucres of this fossil species vary from being highly dissected and spiny like C. wangii and C. ferox to more laminar like C. heterophylla. This similarity is interesting because C. ferox and perhaps also C. wangii are members of section Acanthochlamys, thought to be basal within the genus. Carpinus perryae has asymmetric leaflike bracts that partly enclose an ovate nutlet and, thus, fits within the extant Carpinus subgenus Carpinus, a group with Asian, European, and North American affinities today. Palaeocarpinus, thought to be basal within the Coryloideae, is reported from several Eocene localities in the Okanogan Highlands. These occurrences demonstrate that this primarily Paleocene, extinct genus extended into the Eocene in western North America as it did in Asia. Associated staminate catkins containing coryloid pollen and Corylus-like leaves also occur at Republic along with P. barksdaleae. The presence in the Okanogan Highlands floras of a suite of coryloid plants including both extinct and extant genera demonstrates that, like the birch subfamily Betuloideae, the subfamily Coryloideae was also a significant and diverse group in western North America during the middle Eocene.

Keywords: Betulaceae, Carpinus, Coryloideae, Corylus, Palaeocarpinus.

Introduction

The Betulaceae is a primarily Northern Hemisphere temperate family that includes the birches (Betula), alders (Alnus), hop hornbeams (Ostrya), ironwoods (Carpinus), hazelnuts (Corylus), and the Chinese endemic shrub, Ostryopsis (Mabberley 1990). The six extant genera are traditionally placed in two subfamilies, the Betuloideae (Alnus, Betula) and Coryloideae (Carpinus, Corylus, Ostrya, Ostryopsis), a phylogenetic organization that has been strongly supported by recent studies on the basis of rbcL, ITS, morphology, and various combined data sets (Piguet et al. 1992; Savard et al. 1993; Chen et al. 1999; Whitcher and Wen 2001; Yoo and Wen 2002). Extant genera of the Coryloideae are further divided into the tribes Corylaceae (Corylus) and Carpinaceae (Carpinus, Ostrya, Ostryopsis; Chen et al. 1999).

The family has an extensive fossil record in the Tertiary and is of particular interest as an important component of recent vegetation throughout the Northern Hemisphere. Whereas the earliest reports of the family consist of pollen referred to the genera *Alnus* and *Betula* from the Santonian/Campanian of North America and Japan (Takahashi 1974; Jarzen and Norris 1975; Miki 1977), infructescences and fruits diagnostic of these extant genera are not confirmed before the Eocene. The origin and diversification of extant genera is best documented by megafoils from the Early Tertiary (Crane 1989; Chen et al. 1999; Manchester 1999; Whitcher and Wen 2001). During this time, we see the earliest known occurrences of most modern genera and the presence of several extinct forms including *Palaeocarpinus*, *Asterocarpinus*, *Coryloides*, and *Cranea*, genera that appear to occupy a variety of basal and intermediate evolutionary positions within the Coryloideae. *Cranea*, from the Paleocene of western North America, bears similarities to the extant Chinese endemic genus *Ostryopsis* (Manchester and Chen 1998). The Late Eocene to Oligocene *Asterocarpinus*, also from western North America, resembles *Carpinus* and *Ostrya* in some features but has a unique radiating, multilobed, involucral wing (Manchester and Crane 1987). *Palaeocarpinus* is a widespread, primarily Paleocene genus of western North...
America, Asia, and Europe that combines coryloid characters representative of both tribes, Coryleae and Carpineae, indicating its possible basal and/or ancestral position in coryloid evolution (Crane 1981; Chen et al. 1999; Manchester 1999).

In recent years, studies of Paleogene fossils have greatly increased our knowledge of the early fossil history of both subfamilies of the Betulaceae. Co-occurring betulaceous infructescences, fruits, staminate catkins, pollen, and leaves are known from a number of localities in Europe, Asia, and western North America. Whereas coryloid leaf and pollen remains from different sites tend to be quite similar, fossil fruits provide the most diagnostic characters that delimit both extinct and extant genera. Floras of the middle Eocene Okanogan Highlands contain several coryloid taxa including both fertile and vegetative remains. Some of these have been previously illustrated (Crane 1989; Wehr and Hopkins 1994; Wehr 1995; Pigg and Wehr 2002) and mentioned in reviews (Wehr 1994; Wehr and Manchester 1996; Chen et al. 1999; Manchester 1999; Whitcher and Wen 2001), but the taxa have not been formally named. In this contribution, we describe five species of fruits and document an associated staminate catkin, all corresponding to the subfamily Coryloideae (Betulaceae) from the middle Eocene Republic flora of northeastern Washington State and related sites in British Columbia. The new taxa include Corylus johnsonii sp. nov. and Carpinus perryae sp. nov. from the Republic flora, which are the oldest known occurrences of these two living genera. Palaeocarpinus is represented by three new species, Palaeocarpinus barksdaleae sp. nov. from Republic; Palaeocarpinus stonebergae sp. nov. from Princeton, British Columbia; and Palaeocarpinus dentatus comb. nov. from Stump Lake, British Columbia, demonstrating that this extinct genus known best from the Paleocene persisted into the Eocene of western North America.

Material and Methods

The specimens described herein are from several sites in and near Republic, Washington (Klondike Mountain Formation); Princeton, British Columbia, Canada (Allenby Formation); and four additional sites in British Columbia (fig. 1; table 1). From 40Ar to 39Ar dating, the Klondike Mountain Formation in the Republic district is 50–49 Ma (B. Berger, written communication, 1992). The Allenby Formation and other occurrences in British Columbia are also of Eocene age (Crane and Stockey 1987; Stockey and Manchester 1988; Archibald and Mathewes 2000). Other constituents of these floras have been treated separately (e.g., Wolfe and Wehr 1987; Wehr and Hopkins 1994). The Stump Lake locality was collected in the late 1980s by the Canadian Geological Survey (Dawson 1890; Penhallow 2000). One specimen is housed in the Redpath Museum, McGill University, Montreal, Canada, and was reexamined by one of us (K. B. Pigg). Two additional incomplete specimens from Stump Lake were photographed by one of us (S. R. Manchester) at the Canadian Geological Survey in Ottawa. Leaves of apparent coryloid affinity occur at most of these localities (Wehr and Hopkins 1994, their fig. 1), but there remains uncertainty as to which kinds of leaves correspond to each of the fruit types treated here, and we consider them to be outside the scope of our present investigation.

Megafossil specimens were degaged for critical features and photographed with reflected light using low-angle light to enhance fine details. Pollen was recovered from catkins by removing small fragments of carbonaceous material, cleaning in HCl and HF, and washing in water. Pollen was macerated gently by placing a drop of ammonia into water containing the fragments while observing them with a dissecting microscope. As the opaque material cleared, in ca. 30 s, more water was added to stop the reaction. Specimens were washed in water until neutral pH, were prepared by standard techniques, and were mounted on slides for light microscopy and on stubs for SEM. Digital images were processed using Adobe Photoshop 7.0.

Specimens are housed at the Burke Museum of Natural History and Culture, Seattle, Washington (UWBM); Stonerose Interpretive Center, Republic, Washington (SR); Florida Museum of Natural History, Gainesville, Florida (UF); Redpath Museum, McGill University, Montreal, Quebec, Canada (RM); and the Canadian Geological Survey, Ottawa, Ontario, Canada (GSC).

Systematics

Family—Betulaceae

Genus—Corylus L.

Type Species—Corylus avellana L.

Corylus johnsonii Pigg, Manchester et Wehr, sp. nov. (figs. 2A–2], 3A–3L, 4A–4H)

Specific diagnosis. Infructescence bearing two to three nuts, more or less terminal on stout peduncle; nut ovoid to almost circular in outline, 8–17 mm in diameter, surrounded by involucre of two bracts; involucre up to 20 mm long and 17 mm wide, entire at base, not obviously parted for basal 2/3 of its length, divided distally into lobes for distal 1/3 of

Fig. 1 Map of the Okanogan Highlands region. Numbers indicating localities are listed in table 1.
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Table 1

Distribution of Coryloid Fruits among Eocene Localities of the Okanogan Highlands, Washington, and British Columbia

<table>
<thead>
<tr>
<th>Locality</th>
<th>Corylus johnsonii</th>
<th>Carpinus perryae</th>
<th>Palaeocarpinus barksdaleae</th>
<th>Palaeocarpinus stonebergae</th>
<th>Palaeocarpinus dentatus</th>
<th>Palaeocarpinus sp.</th>
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<tr>
<td>2. Boot Hill, Republic, Washington, UWBM locality B4131</td>
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<td>4. Gold Mountain, Republic, Washington, UWBM locality B5077</td>
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<td>5. Resner Canyon, Washington, UWBM locality B1795</td>
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<td>7. Corkscrew Mountain, Washington, UWBM locality B6494</td>
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<td>10. Quilchena, British Columbia (Archibald and Mathewes 2000)</td>
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<td>11. Stump Lake, British Columbia (Penhalloow 1908)</td>
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<td>13. Smithers, British Columbia, UWBM locality B1690</td>
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Note. See figure 1 for locations on map.

Its length, subsidiary lobes sometimes present, bracts covered with small spines 1–2.5 mm long, irregular, sometimes branched; bract venation of numerous parallel veins that divide and occasionally fuse in bracts and extend into lobes. Fruit wall composed of elongate fiber-like anastomosing sclereids.

Derivation of specific epithet. The specific epithet, johnsonii, is proposed in honor of Kirk R. Johnson, for his recognition of the significance of the Republic flora and fauna and his vigorous collecting and ongoing involvement in its development.

Holotype. SR 98-1-2A&B (fig. 2A).

Paratypes. SR 99-8-33 (fig. 2B); UWBM 77714 (fig. 2C); SR 96-2-2 (figs. 2D, 3L); UWBM 78140A (fig. 2E; fig. 4A, 4E); SR 99-5-5 (fig. 2F); SR 98-9-4 (fig. 2G); UF18152-26084 (figs. 2H, 4D); UWBM 96135A (fig. 2l); SR 93-8-13 (fig. 2J); UWBM 94591 (fig. 3A; fig. 4B, 4G); SR 97-4-4A (figs. 3B, 4C); SR 94-4-6 (fig. 3C); SR 96-11-24 (fig. 3D, 3G); UWBM 95515 (fig. 3E); UWBM 71062A (figs. 3F, 4H); SR 99-5-21B (fig. 3H); SR 99-7-10 (fig. 3I, 3J); UWBM 26040A (figs. 3K, 4F).

Type locality. Corner Lot (10th and Clark streets), Republic, Washington (A0307 B).

Age and stratigraphy. Middle Eocene Klondike Mountain Formation, 50–49 Ma.

Results. The description of Corylus johnsonii is based on 34 specimens found at the Corner Lot and Boot Hill localities of the Republic flora (table 1). The specimens include 12 infructescences with attached involucres containing either nuts or casts of nuts (fig. 2A–2D, 2F, 2G; fig. 3A, 3E, 3I), 14 involucres (fig. 2E, 2L, 2J; fig. 3B–3D, 3F, 3G), and eight isolated specimens of paired or individual nuts (fig. 3H, 3K; fig. 4F). These specimens show an intergradational sequence in shape and dissection of involucral lobes from those with what spined (fig. 3B, 3C, 3F) to those with an extensive network of lateral spines (fig. 2A–2H, 2J; fig. 3D, 3E; fig. 4A). Involucral lobes also range in appearance from thin and leafy with well-preserved venation (figs. 3F, 4H) to others that are considerably thicker with obscure veins (fig. 2A, 2B; fig. 3B; fig. 4C). Specimens are fractured at different levels. Some show the outer surface of the involucral bracts (fig. 2A, 2B, 2J; fig. 3B; fig. 4C), and others show a subsurface layer through the bract revealing a helically arranged pattern of spinelike protruberances, probably the points of spine attachment (figs. 3A, 4B). In other specimens, the nut surface is exposed and appears relatively smooth with longitudinal lines (fig. 2A; fig. 3C, 3I, 3K; fig. 4F). Still other specimens are fractured or abraded to reveal subsurface layers of the pericarp, which appears to be composed of elongate, somewhat anastomosing fiber-like sclereids (fig. 3L). Other specimens may represent molds of the fruits that have filled with sediment casts showing the initial shape of the replaced fruit. Many specimens show a combination of different layers.

The most complete specimens are infructescences composed
Fig. 2 *Corylus johnsonii* sp. nov. infructescences from Corner Lot and Boot Hill, Republic, Washington, to show range of variation. A–E, ×1.5. F–J, ×1.8. A, Holotype specimen showing paired involucres on long peduncle. Note smooth surface of nut (top) and multilobed, spiny dissected involucre (bottom) and position of lateral scars (arrow), photograph inverted, SR 98-1-2A. B, Paired, highly dissected involucres on peduncle, SR 99-8-33. C, Single involucre attached to peduncle, UWBM 77714. D, Specimen showing details of involucre containing nut and long peduncle, SR 96-2-2. E, Specimen with highly dissected involucre (left) and nut (right). Note long peduncle, probably originally in attachment (arrow), UWBM 78140A. F, Highly dissected involucre attached to peduncle, SR 99-5-5. G, Paired involucres with highly dissected surface, SR 98-9-4. H, Involucre with forked spines (left), UF18152-26084. I, Involucre showing three major lobes, UWBM 96135A. J, Paired involucres with primarily simple spines, SR 93-8-13.
Fig. 3  *Corylus johnsonii* sp. nov. involucres on peduncles, individual involucres, and paired and isolated nuts to show variation. A–F, × 1.8. 
A, Infructesence showing paired involucres in attachment to stout peduncle. Note attachment scar (arrow), UWBM 94591. B, Involucre showing five lobes covered with spines, SR 97-4-4A. C, Two nuts partly contained in paired involucres, SR 94-4-6. D, Involucre subtended by long peduncle, probably originally in attachment, SR 96-11-24. E, Paired nuts in involucres attached to peduncle, UWBM 95515. F, Involucre with relatively smooth outline and laminar lobes, showing only a few spines (arrow), UWBM 71062A. G, Higher magnification of specimen illustrated in D after further dégagement, showing remnants of style, SR 96-11-24, × 6.2. H, Isolated nut, SR 99-5-21B, × 1.8. I, Paired nuts on peduncle. Note nut surface on left and small leafy appendages, SR 99-7-10, × 1.8. J, Detail of leafy structure on peduncle in I, SR 99-7-10, × 2.3. K, Detail of attachment scar from fig. 2D, SR 96-2-2, × 2.8. L, Detail of nut surface from fig. 2D, × 10.6.

of paired, attached involucres containing nuts and borne on a stout peduncle 1.3 mm wide and incomplete but at least 4.4 cm long (fig. 2A, 2D, 2F; fig. 3A, 3E, 3J). Two specimens have paired involucral heads positioned above the peduncles on which they were probably attached (figs. 2E, 3D). On several specimens, there is a pair of lateral scars preserved ca. 8–23 mm below the attached fruits (figs. 2A, 3A, 4G). One specimen shows a pair of small leafy appendages attached at a comparable position (fig. 3I, 3J). These might be the primary bracts of each cymule, whereas the involucres are hypothesized to be derived from fused tertiary bracts or fused tertiary plus secondary bracts. Most specimens consist of paired involucres.
Fig. 4 Corylus johnsonii sp. nov. detail. A, Higher magnification of fig. 2E showing detail of involucre, UWBM 78140A, x 2.5. B, Higher magnification of fig. 3A showing detail of involucre heads and helically arranged spinelike pattern on subsurface of involucre (left), UWBM 94591, x 2.4. C, Higher magnification of fig. 3B showing vertical stripes on body of involucre, SR 97-4-4, x 1.8. D, E, Detail of spines on involucre bodies. Higher magnification of fig. 2H and 2E, respectively, UF18152-26084, x 5.3. F, Higher magnification of specimen in fig. 2D and fig. 3K showing detail of attachment scar on surface of nut, UWBM 26040A, x 3. G, Detail of fig. 3A showing peduncle with attachment scar (arrow), UWBM 94591, x 3.9. H, Detail of fig. 3F showing venation of involucre lobes (numbered), UWBM 71062A, x 3.2.

containing ovoid nuts or casts, but several nuts are also found either paired or isolated in the matrix (fig. 3H, 3K; fig. 4F). The basal attachment scar is oval and covers a relatively small portion of the nut (figs. 3K, 4F). Several specimens show evidence of a distal scar in the position of former style attachment, and in one case, small remnants of the style are preserved (fig. 3G).

Involucres are up to 20 mm long and 17 mm wide, not obviously parted for the basal 2/3 of their length and lobed distally. Some of the lobes bear occasional short and often poorly differentiated subsidiary lobes (fig. 4H). On the basis of the best-preserved areas of the bract, it is estimated that each bract has ca. 16 longitudinal veins. The most prominent veins supply the major apical lobes, while subsidiary lobes and teeth are vascularized by smaller veins (fig. 4H). Other longitudinal veins branch and become less distinct toward the involucre apex. Among the fruits with more dissected involucres, some appear to have mostly simple spines (figs. 2J, 3E), while others are densely clothed with both simple and branched spines (fig. 2A–2H; fig. 3B, 3D; fig. 4A, 4C–4E).

Discussion. Corylus (hazelnut, filbert) includes ca. 15–20 species that occur throughout the Northern Hemisphere, primarily in Asia but also in Europe and North America (Whitcher and Wen 2001). Corylus americana, the common American hazelnut, is known from eastern and midwestern North America. The primarily North American species Corylus cornuta also occurs in eastern North America and Corylus californica in California. In Europe, the type species, Corylus avellana, occurs, along with a variety, C. avellana var. pontica. The Turkish hazel, Corylus colurna, and the filbert, Corylus maxima, are native to southern Europe and western Asia, and Corylus jacquemontii is native to the western Himalayas.
Around 10 species occur in eastern Asia, Japan, China, and the Himalayas including Corylus chinensis, Corylus fargesii, Corylus heterophylla, Corylus ferox, Corylus sieboldiana, Corylus tibetica, and Corylus wangii (Whitcher and Wen 2001).

Species delimitation within Corylus has not been consistent; however, most authors have traditionally recognized two or three major infrageneric divisions at the rank of either subgenus or section (Whitcher and Wen 2001). Most recent analyses combining molecular markers and morphological data support the division of the genus into two sections, section Acanthochlamys and section Corylus, the latter of which is further divided into three subsections. Section Acanthochlamys has traditionally been considered basal on the basis of morphological data, and this phylogeny is supported by nuclear ITS and chloroplast rbcL markers (Erdogan and Mehlenbacher 2000; Forest and Bruneau 2000; Whitcher and Wen 2001). This section includes C. ferox, a species with spiny involucres apparently lacking laminar lobes, and probably C. wangii, which has a more laminar involucre with fewer spines (Whitcher 1999; Whitcher and Wen 2001).

The range of variability in C. johnsonii includes specimens resembling three extant species of Corylus: C. wangii, C. ferox, and C. heterophylla. Those similar to C. wangii have involucres with narrow lobes that bear both numerous branched and unbranched spines (fig. 2), those like C. ferox have a highly prickly involucre surface (fig. 3E), and those resembling C. heterophylla are smoother with narrow, finger-like lobes in which vascular tissue is clearly seen (figs. 2F, 3H). Two of these species, C. ferox and C. heterophylla, are known to occur sympatrically in Sichuan province in China today (J. Wen, personal communication, 2003). We recognize this variability among our 34 specimens; however, on close examination, it is clear that these three morphotypes intergrade such that it is difficult to decide whether multiple morphologically overlapping taxa or a single highly variable species is represented. For example, when the smooth, C. heterophylla-like involucre (figs. 3F, 4H) was first found, it was thought to be a distinctive species until degagement of the surrounding matrix revealed a few spines like those in other specimens (fig. 3F, left). Whereas some specimens bear mostly branched spines and fewer elongate unbranched ones (e.g., fig. 2E, 2G, 2H; fig. 4A), in other specimens, the inverse is true (fig. 2J). The problem is compounded by the differential preservation among specimens. Some involucres that appear to lack abundant spines may be only partially preserved and/or incompletely prepared. Other specimens that have more elaborate involucres (fig. 2A) may simply be more completely preserved. Still others are more difficult to interpret because they are fractured through the specimen and show various internal layers (fig. 2D) or have surfaces that appear to have been degraded during weathering and/or the preservation process (fig. 2I; fig. 3A, 3I).

Although we acknowledge that our concept of C. johnsonii encompasses a wide range of morphological variability, we choose to include this entire suite of specimens within this species and suggest that perhaps this middle Eocene form may contain a mosaic of features that later became more clearly delineated within extant species. Both of the more spiny extant species discussed above, C. wangii and C. ferox, have also been compared with the typically spiny fossil genus Palaeocarpinus (Crane 1981; Chen et al. 1999; Manchester 1999). Corylus johnsonii sp. nov. represents the stratigraphically oldest unequivocal evidence of the genus Corylus on the basis of a combination of features including cupulate infructescences borne in paired involucres on elongate peduncles, fruits in paired involucres, and isolated nuts. Small, isolated nuts lacking involucres previously referred to Corylus have been recovered from the Paleocene of England, Greenland, and Montana (Seward and Holttum 1924; Brown 1962; Koch 1978).

Although these specimens appear to have coryloid affinities, without the subtending infructescence, it is difficult to determine whether they represent isolated fruits of Corylus, Palaeocarpinus, or perhaps some other extinct taxon. The most convincing of these specimens, Corylus insignis, is only 5 mm in diameter but shows evidence of a characteristic Corylus attachment scar (Brown 1962; Crane 1989). Larger silicified nuts, 24–37 mm in diameter, from the middle Eocene Clarno Nut Beds of Oregon, have been referred to the genus Coryloides because of their anatomical and morphological similarities to Corylus, but they differ in being spherical rather than ovate like typical extant forms (Manchester 1994, 1999). Corylus has also been reported on the basis of well-preserved nuts from the Oligocene of Kazakhstan (Dorofeev in Takhtajan 1982), Corylocarpinus from the Pliocene of Willershausen, Germany, has a pedicellate nut and involucre that show similarities both to Corylus and Carpinus but is not well understood because it is based on a single impression specimen (Strauss 1969).

Other fossil coryloid remains are difficult to place taxonomically with certainty. Leaves identified as Corylus and catkins with in situ pollen indistinguishable from extant Corylus are often known in association with Palaeocarpinus in North America and China (Manchester and Chen 1996). It may be that these features are more morphologically conservative than pistillate reproductive structures.

Genus—Carpinus L.

Type Species—Carpinus betulus L.

Carpinus perryae Pigg, Manchester et Wehr sp. nov. (fig. 5A, 5C)

Specific diagnosis. Fruit an ovate nutlet 5.5–6.0 mm high, 3.3–4.0 mm, borne at base of elongate, obovate, slightly asymmetrical unlobed winglike bract; bract 22–25 mm long, 6–8 mm wide; primary veins five to six, radiating from base of wing and leading into teeth; thickest primary vein asymmetrically positioned, running toward apex; additional three to four primary veins on wider side; one to two on narrower side; secondary veins alternately produced by primaries, tertiaries connecting them at right and acute angles; margin with few, distantly spaced teeth; teeth right angled to obtuse, sometimes almost spiny, vascularized by either primaries or seconds, sinuses rounded.

Derivation of specific epithet. The specific epithet, perryae, is named in honor of Madilane Perry for her role in the founding of the Stonerose Interpretative Center, Republic, Washington.
Fig. 5  *Carpinus perryae* sp. nov. fertile bracts from Knob Hill, Republic, Washington, with attached nutlets and extant *Carpinus cordata* var. *cordata* Bl. fertile bract (labeled *C. erosa*, UF modern fruit reference collection 167).  A, Fossil showing detail of marginal teeth, UWBM 71171, ×5.  B, Extant *C. cordata* var. *cordata* showing detail of marginal teeth, ×5.4.  C, Holotype specimen (right) and paratype (left), UWBM 71171, ×2.5.  D, Extant *C. cordata* var. *cordata* fertile bract, ×3.

Holotype.  UWBM 71171, specimen A (fig. 5A, 5C).
Paratype.  UWBM 71171, specimen B (fig. 5C).


Age and stratigraphy.  Middle Eocene Klondike Mountain Formation, 50–49 Ma.

Results.  *Carpinus perryae* is represented by two isolated fruits occurring side by side on a single slab of shale (fig. 5C) from Knob Hill, Republic, Washington (table 1).  There is no evidence of the infructescence axis or the mode of fruit attachment.  Fruits are ovate nutlets 5.5–6 mm high × 3.3–4.0 mm wide surrounded by an elongate, obovate, asymmetrical winglike bract 22–25 mm long × 6–8 mm wide that arises apically from the nutlet (fig. 5C), resembling that of some extant species (e.g., *Carpinus cordata* var. *cordata*; fig. 5B, 5D).  Five to six primary craspedodromous veins radiate out from the basal area of attachment to vascularize the bract, with three to four veins on the wider side and one to two on the narrower side.  Veins branch alternately from the primaries and are interconnected by tertiaries at right and acute angles.  The bract is unlobed (fig. 5C), and the margin has small, distantly spaced marginal teeth on both its concave and convex sides (fig. 5A, 5C).  Teeth are vascularized by either the primary veins or secondary veins that fork at an acute angle from the primaries (fig. 5A, 5C).

Discussion.  The genus *Carpinus* is composed of ca. 35 species distributed today throughout the temperate Northern Hemisphere including Europe, eastern North America, and especially eastern Asia.  This genus includes the hornbeam, *Carpinus betulus* of Britain; the American hornbeam, *Carpinus caroliniana* of eastern North America; and *Carpinus cordata* and *Carpinus laxiflora* of eastern Asia (Furlow 1990; Mabberley 1990; Yoo and Wen 2002).  Historically, the genus has been subdivided on the basis of fruit and seed morphology most commonly into two subgenera, *Distegicarpus* and *Carpinus*, sometimes recognized at the level of section.  These have in turn been divided into additional groupings of varying composition by different authors.  Recent ITS studies (Yoo and Wen 2002) have suggested that the genus *Carpinus* is paraphyletic, with the closely related genus *Ostrya* nested within the two sections of *Carpinus*, while morphological data support the genus *Carpinus* as monophyletic.  In the Yoo and Wen analysis, section *Distegicarpus* occupies a basal position in the genus, and section *Carpinus* is monophyletic.

Yoo and Wen (2002) performed a morphological analysis based on 23 characters of infructescence, nutlet, fruit bract, seed, and leaves.  Those of their characters that can be coded for the Republic fossil *C. perryae* include: (8) nutlet shape, (10) fruit bract symmetry, (11) fruit bract enclosure of nutlet, (12) fruit bract lobe number, (13) serration of middle bract lobe, and (16) shape of fruit bracts.  On the basis of these characters, *C. perryae* fits easily within section *Carpinus* and shares with this section synapomorphies including asymmetrical bracts that partly enclose an ovate nutlet.  This combination of features also occurs within the following extant species: *Carpinus cornea*, *Carpinus hupeana*, *C. laxiflora*, *Carpinus monbeigiana*, *Carpinus orientalis*, *Carpinus pubescens*, and *Carpinus putoensis*.  However, one difference between *C. perryae* and extant members of the genus is the obovate rather than ovate shape of the leafy bract.  We did not
observe a characteristic longitudinal striation typical of many extant *Carpinus* nutlets in *C. perryae*, but this could be due to the nature of preservation.

*Carpinus perryae* is the oldest known example of the genus to date. *Carpinus*-like bracts described as “still debatable,” along with betulaceous pollen, are known from the late Middle Eocene of Germany (Wilde and Frankenhäuser 1998). Fossil *Carpinus* has been reported from the late Eocene and early Oligocene of Japan (Tanai 1972; Uemura and Tanai 1993) as well as the Oligocene and younger floras of Europe (Berger 1953; Mai 1995) but is considerably rarer in western North America (Manchester 1999). Asian fossils of early Oligocene to Neogene age are very similar to extant members of *Carpinus* section *Distegocarpus*, which is today endemic to eastern Asia, and suggest that this section radiated by the Oligocene in Asia (Yoo and Wen 2002). It is interesting that *C. perryae* is more similar to the larger *Carpinus* section *Carpinus* clade, suggesting that this group was already established in western North America by the middle Eocene.

**Genus**—Palaeocarpinus Crane

**Type Species**—Palaeocarpinus laciniata Crane

Palaeocarpinus barksdaleae Pigg, Manchester, et Wehr, sp. nov. (fig. 6)

**Specific diagnosis.** Fruit an elliptical to ovate nutlet subtended and enveloped by a pair of fan-shaped bracts; bracts 6–11 (x = 7.9 mm, n = 22) mm wide, 4.5–10 (x = 7.5 mm, n = 22) mm high, foliar, and ending distally with distinct spiny tips; sinuses between teeth of more or less equal width; bracts with ca. 12 primary veins radiating from base leading into spines; adjacent primary veins connected by network of reticulate elongate areoles formed by secondaries and tertiaries; some secondaries terminating in spines, others forming brochiodydromous loops within the bract margin (fig. 6, 6H–6J). Bracts have ca. 12 primary veins radiating from the base, forking distally, and leading into spiny tips (fig. 6H–6J). Adjacent primary veins are connected by a network of secondary and tertiary veins that form a reticulum of elongate areoles ca. 1 mm long x 0.5 mm wide (fig. 6C, 6H–6J). Some secondaries terminate in spines (fig. 6H, 6J), while others form brochiodydromous loops within the bract margin (fig. 6C, 6J). The nutlet is typically 2.5–5 (x = 3.6) mm high, 1.3–3.2 (x = 1.4, n = 17) mm wide, 4.5–10 (x = 7.5 mm, n = 22) mm high, foliar, and highly dissected; bract lobes elongate, narrow; distally branched to spiny; nutlet 1.5–5 (x = 2.3, n = 19) mm long, 1.5–4.5 (x = 2.6, n = 18) mm wide, longitudinally ribbed.

**Derivation of specific epithet.** The specific epithet, *barksdaleae*, honors Lisa Barksdale for her incomparable contribution in making the Republic fossils accessible to both the public and scientific community during her 14 yr as curator of the Stonerose Interpretive Center.

**Holotype.** UWBM 97408A & B (fig. 6C, 6E).

**Paratypes.** UWBM 97407A (fig. 6A, 6B); UWBM 97117A (fig. 6D); UWBM 97107 (fig. 6F); UWBM 97114 (fig. 6G); UWBM 74319A (fig. 6H, 6I); UWBM 97113 (fig. 6I); UWBM 74315 (fig. 6K). Not figured: UWBM 97409–97415; UWBM 97108–97112; UWBM 97115–97116; UWBM 97118–97153; UWBM 97262–97276; UWBM 97317–97351; UWBM 97353–97354; ASU 1–5; UF 26689, 26690.

**Type locality.** Gold Mountain (UWBM loc. B5077), Republic flora.

**Age and stratigraphy.** Middle Eocene Klondike Mountain Formation, 50–49 Ma.

**Results.** Palaeocarpinus barksdaleae is based on 90 specimens, each consisting of a nutlet enclosed in paired bracts (fig. 6). Fruits are found isolated in the matrix and not within an infructescence or cymule pair like some Paleocene forms (Crane et al. 1990; Sun and Stockey 1992). Specimens are preserved as part-counterpart or individually and either showing the outer wing (fig. 6G–6K) or inner nutlet side (fig. 6A–6F) of specimens. The species is known from Gold Mountain, Boot Hill, Knob Hill, and Resner Canyon (table 1). It has highly webbed, winglike bracts with major and minor pointed lobes (fig. 6H, 6I, 6K) that extend distally into distinctive pointed tips (fig. 6J).

Each fruit has an elliptical to occasionally ovate, rarely rounded nutlet (fig. 6A–6D, 6F), subtended and enveloped by a pair of fan-shaped bracts (fig. 6F–6I, 6K). The bracts are each 6–11 (x = 7.9 mm, n = 22) mm wide, 4.5–10, (x = 7.5 mm, n = 22) mm high, and distally spiny (fig. 6A, 6H–6J). Bracts have ca. 12 primary veins radiating from the base, forking distally, and leading into spiny tips (fig. 6H–6J). Adjacent primary veins are connected by a network of secondary and tertiary veins that form a reticulum of elongate areoles ca. 1 mm long x 0.5 mm wide (fig. 6C, 6H–6J). Some secondaries terminate in spines (fig. 6H, 6J), while others form brochiodydromous loops within the bract margin (fig. 6C, 6J). The nutlet is typically 2.5–5 (x = 3.6) mm high, 1.3–3.2 (x = 1.4, n = 17) mm wide, with four to five prominent longitudinal ribs (fig. 6A, 6C, 6D). Some nutlets are rounded in outline (fig. 6D, 6F), but they are less common than the elongate forms (fig. 6A–6C). Where preserved, the base of the nutlet is flattened (fig. 6C, 6D), and there is no evidence of an elongate peduncle. Several fruits retain a style up to 1 mm long x 0.3 mm wide (fig. 6E), but a distal bifurcation, as seen in *Palaeocarpinus joffrensis* (Sun and Stockey 1992), was not recovered.
Fig. 6  *Palaeocarpinus barksdaleae* sp. nov. from Boot Hill, Knob Hill, and Gold Mountain, Republic, Washington. A–D, × 7. F, H, × 4.5. G, I, K, × 6. A, Fruit impression showing inner side of bract. Counterpart of fig. 5B, UWBM 97407B. B, Fruit showing inner side of bract with elliptical nutlet. Counterpart of fig. 5A, UWBM 97407A. C, Holotype specimen. Fruit showing inner side of bract with elliptical nutlet. Note flattened base, striations on nutlet surface, and details of bract venation, UWBM 97408A. D, Ovate-rounded fruit showing inner side of bract with rounded nutlet. Note striations on surface, UWBM 97117A. E, Detail of apical portion of holotype specimen showing style (arrow). Counterpart of C, UWBM 97408B, ×15. F, Fruit from inner side of bract, showing rounded nutlet, UWBM 97107. G, Fruit showing inner side of bract, UWBM 97114. H, Fruit showing outer side of bract and well-preserved veins radiating from base into reticulum of veins ending in spiny tips, UWBM 74319A. I, Fruit from outer side of bract showing well-defined, pointed primary and secondary lobes with sharp tips and reticulate venation, UWBM 97113. J, Higher magnification of specimen in H showing detail of venation and pointed tips of lobes, UWBM 74319A, ×17. K, Specimen fractured to show both outer bract side (left) and inside of adjacent bract with imprint of ovate nutlet (right), UWBM 74315.
spicuously absent from the better-known nearby paleobotanical locality of One Mile Creek (Crane and Stockey 1987). The specimens are found individually in the matrix, and there is no evidence of paired fruits or ones in attachment to their infructescence axis. Each fruit includes an elliptical to circular nutlet (fig. 7) subtended and surrounded by a pair of highly dissected fan-shaped bracts. The nutlet is 1.1–5 (, x 2.3) mm long and 1.5–4.5 (, ) mm wide, with 10 elongated, narrow, pointed lobes radiating out from the base (fig. 7) that become branched and spiny at their tips (fig. 7D–7F) with occasional dichotomies and sometimes with branching lateral spines (fig. 7A,7F). The bracts are planar but lack much fusion or webbing of laminar material (fig. 7).

In contrast to P. barksdaleae, P. stonebergae fruits are somewhat smaller, and, although similar in basal areas of the bract, the bracts are much more highly dissected and are more burr-like than winglike. Palaeocarpinus stonebergae bracts are similar to those of an undescribed species from the Eocene Clarno Formation of Oregon (Manchester 1994, plate 8, fig. 20) in their small size and lack of webbing. However, the Clarno species has bracts with only about five radiating spines.

Palaeocarpinus dentatus (Penhallow) Pigg, Manchester et Wehr, comb. nov. (fig. 8A)

**Synonymy.** Carpolithes dentatus Penhallow (in Dawson 1890, fig. 26).

**Specific diagnosis.** Fruit, including bract, 8 mm long × 10 mm wide; nutlet 4 mm long × 2 mm wide, elliptical, apex acute, base flattened; bract margin strongly toothed, teeth acute, sinuses broad toward base, narrower at apex; veins prominent.

**Derivation of specific epithet.** The specific epithet, dentatus, refers to the toothed margin of the bract.

**Lectotypy.** Penhallow (in Dawson 1890) did not designate a holotype, but the line diagram (Dawson 1890, fig. 26) was probably based in part on Redpath Museum specimen 2.2420 (our fig. 8A) and was originally collected by G. M. Dawson in 1888 and donated by the Geological Survey of Canada.

**Type locality.** Stump Lake (Quilchena area), British Columbia, Canada.

**Age and stratigraphy.** Middle Eocene.

**Results.** Palaeocarpinus dentatus (Penhallow) Pigg, Manchester & Wehr comb. nov., was initially described from several specimens from Stump Lake, British Columbia. Fruits including the bracts are a little more than 8 mm high × 10 mm wide (fig. 8A). The nutlet is 4 mm long × 2 mm wide and elliptical, with a flattened base. The bract is incompletely preserved but extends to the margin in the upper left (fig. 8A), demonstrating the shape of bract lobes and presence of elongate marginal spines. Major orders of venation are strong, and there is some indication of smaller vein reticulation (fig. 8A). Lobes of the bract are separated by sinuses that appear broader toward the base and more narrow apically in areas where the margin is preserved.

Several additional specimens referable to the genus Palaeocarpinus are known from other sites in the Okanagan Highlands (table 1), but because they are known from only one or

A, Palaeocarpinus dentatus (Penhallow) comb. nov., Stump Lake, British Columbia. This specimen was provisionally called Carpolithes dentatus by Dawson (1890) and used by him in his line diagram reconstruction. Note elliptical nutlet, partly preserved bract with wide venation; Redpath Museum RM 2.2420. B–D, Palaeocarpinus spp. B, Quilchena, British Columbia, showing rounded nutlet enclosed in partly preserved bract with fine radiating venation; GSC 76997. C, Golden Promise Mine, Washington. Note large, robust form; winglike bract; and extensive spiny tips; UWBM 57477A. D, Corkscrew Mountain, Washington. Note elongate wing and elliptical nutlet.

a few specimens that do not show all critical features in each instance, we are unable to assign them confidently to species. One from Quilchena, British Columbia, has a rounded and striated nutlet surrounded by a partly preserved wing with many fine veins radiating out from the nutlet (fig. 8B). A fruit from Corkscrew Mountain (fig. 8D) is winged and has an elliptical nutlet and generally resembles P. barksdaleae except that the shape of the wing is more elongate and similar to those of the Russian Palaeocarpinus sikhotealinensis. Additional material occurs at Horsefly, British Columbia (not figured), and Smithers, British Columbia (not figured). A distinctive specimen from the Golden Promise Mine of the Republic flora is considerably larger and more robust than the other Eocene forms (fig. 8C). This specimen is 15 mm long, more than 20 mm wide, and has a transitional morphology between P. barksdaleae and P. stonebergae with bracts that are winglike, like those of P. barksdaleae (fig. 6), but bears highly dissected spines like those of P. stonebergae (fig. 7).

Discussion. Palaeocarpinus was created in 1981 by Crane for coryloid fruits that showed intermediate features between Corylus and Carpinus. This genus is distinguished by the presence of a striated nutlet enclosed in two more or less equally sized bracts with some evidence of a perigone bearing simple trichomes (Crane 1981). Representatives are currently known from at least a dozen Paleocene localities in Asia, Far East Russia, England, France, and, in western North America, Montana, North Dakota, and Alberta, Canada (Crane 1981, 1989; Crane et al. 1990; Sun and Stockey 1992; Manchester and Chen 1996; Manchester and Guo 1996; Akhmetiev and Golovneva 1998; Chen et al. 1999; Manchester 1999; S. Manchester, K. Pigg, and P. Crane, unpublished data). One species is known from the Late Eocene–Early Oligocene of Far East Russia (Akhmetiev and Manchester 2000).

Paleocene occurrences include the type species Palaeocarpinus laciniata from the Reading and Woolrich Beds in England (Crane 1981); an unnamed species from Menat, France (de Saporta and Marion 1883; Laurent 1912; Crane 1981); P. joffrenensis of central Alberta and additional localities in western North America (Sun and Stockey 1992; S. R. Manchester, unpublished data); Palaeocarpinus aspinosa from Wyoming (Manchester and Chen 1996); an unnamed species from Almont and Beicegel Creek, North Dakota (Crane et al. 1990; S. Manchester, K. Pigg, and P. Crane, unpublished data); Palaeocarpinus orientalis from China (Manchester and Guo 1996); and Palaeocarpinus pacifica from Far East Russia (Akhmetiev and Golovneva 1998). A younger species, P. sikhotealinensis, has been described from the Upper Eocene/Oligocene of Far East Russia (Akhmetiev and Manchester 2000). Several additional unnamed forms are currently under study (S. R. Manchester, unpublished data).

Species of Palaeocarpinus are best delineated on combinations of morphological characters. Whereas some species (e.g., P. joffrenensis) are widely distributed, other distinctive forms (e.g., the Almont/Beicegel Creek material) are known from only a few localities. Given these patterns, it is not always clear where to draw the lines of species delimitation, particularly when only one or two specimens are known from a given site and preservation may not allow for determination of critical features. An understanding of the overall diversity and distribution of characters within this genus is still in flux.

Palaeocarpinus laciniata (Crane 1981) has about five large, spiny lobes, and the preservation of cuticular details generally
is not known for other species. The unnamed species from Menat is similar to *P. laciniata*, with somewhat webbed, wing-like bracts and has a characteristically long peduncle. Whereas these two species and the Paleocene species from Far East Russia, *P. pacifica*, are known only from isolated fruits, the other Paleocene forms (*P. joffrensis*, *P. orientalis*, *P. aspinosa*) and the Almont/Beicegel Creek form have more details documented for them including infructescence structure, spacing of cy-mules, perianth parts, and, in one case, anatomical structure (Crane et al. 1990; S. Manchester, K. Pigg, and P. Crane, unpublished data).

*Palaeocarpinus joffrensis* was described originally from the Paleocene Joffre Bridge site of Alberta (Sun and Stockey 1992; Hoffman and Stockey 1999), but it is also known in a widespread area of western North America including Montana, Wyoming, and North Dakota (S. R. Manchester, unpublished data). This species usually has numerous, typically elongate dissected lobes with spines and fairly round to oval nutlets that show remnants of a style that branches into two stigmas distally (Sun and Stockey 1992). The fructifications tend to be compact. *Palaeocarpinus orientalis* from northwestern China is quite similar to *P. joffrensis* except for the lack of some comparable features in *P. orientalis* infructescences and differences in associated staminate bract morphology (Manchester and Guo 1998). A distinctive form from western North America, *P. aspinosa*, has more ovoid, leaflike bracts that lack or have only a few teeth on the bract margin. The unnamed species from the North Dakota Almont/Beicegel Creek flora is the largest and has robust, elongate bracts that are highly dissected and toothed (Crane et al. 1990; S. Manchester, K. Pigg, and P. Crane, unpublished data). The range of variability of these North Dakota specimens suggests that several developmental stages are preserved (S. R. Manchester, unpublished data). This is the only anatomically preserved *Palaeocarpinus* currently known and provides the potential for additional anatomical and morphological details. An additional species, *P. pacifica*, was named from a single incomplete specimen from the Paleocene of Far East Russia (Akmetiev and Golovneva 1998).

A younger (Late Eocene to Oligocene) occurrence of the genus is *P. sikhotealinensis* from Far East Russia (Akmetiev and Manchester 2000). *Palaeocarpinus sikhotealinensis* has elongate, winglike bracts with reticulate venation similar to those of many other species (e.g., *P. joffrensis*, *P. orientalis*, and *P. barksdaleae*). The Eocene occurrences of *P. barksdaleae*, *P. stonebergae*, and *P. dentatus*, and *Palaeocarpinus* sp. from additional Okanogan Highlands localities noted both previously (Penhallow 1908) and in this study (fig. 7B–7D), indicate
that the genus was probably widespread in the Pacific Northwest during the early Tertiary.

Several additional fossils recorded from Europe and western North America may represent *Palaeocarpinus*. *Carpinus davisi* from the Tertiary of England (Chandler 1961) is similar to the unnamed Menat species of *Palaeocarpinus* and may warrant further investigation (Crane 1989). Material from western North America described by Brown (1962) and referred to as “burrlike objects” may be assignable to *P. joffrensis*, which is a widely ranging species known from numerous sites in Wyoming, Montana, and North Dakota as well as Alberta (S. R. Manchester, unpublished data). An infructescence illustrated from the Bear Den Member of the Golden Valley flora of North Dakota (Hickey 1977, plate 54, fig. 18) also appears to represent *P. joffrensis*.

**Staminate catkins with coryloid pollen.** Staminate catkins with *in situ* coryloid pollen are known from the Gold Mountain and Boot Hill localities of the Republic flora (fig. 9A, 9B). The first catkin is 30 mm long × 3 mm wide with tightly compact, helically arranged bracts with several pollen sacs attached (fig. 9A). The second specimen is ca. 18 mm long × 3.3 mm wide (fig. 9B). Macerated *in situ* pollen from the first of these is 20 μm in equatorial diameter and 25 μm long with at least three well-developed pores (fig. 9C–9E). Surface ornamentation is minutely punctate (fig. 9E).

**Table 2**

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Note. L = length; W = width.

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**Conclusions**

The presence of *Corylus johnsonii*, *Carpinus perryae*, *Palaeocarpinus barksdaleae* infructescences, fruits, and pollen catkins along with coryloid leaves at Republic, *Palaeocarpinus stonebergae* at Princeton, and similar winged fruits (e.g., *Palaeocarpinus dentatus* and *Palaeocarpinus* sp.) at sites of similar age in other parts of British Columbia demonstrates that subfamily Coryloidae of the Betulaceae was well represented in the middle Eocene floras of the Okanagan Highlands. Both the extant genera *Corylus* and *Carpinus* and three species of the morphologically intermediate extinct genus *Palaeocarpinus* are recognized in these floras. This study thus shows that while *Palaeocarpinus* may have been more widespread in the Paleocene, the genus persisted and diversified in the Eocene of western North America. The presence in the Republic flora of the oldest known examples of *Corylus* and *Carpinus* demonstrates that *Palaeocarpinus* overlapped with the modern genera and suggests that the split into what we now recognize as the tribes Coryleae and Carpinaceae within subfamily Coryloidae had occurred by the Eocene, with remnants of early forms persisting. The youngest *Palaeocarpinus* species currently known are Asian Eocene/Oligocene forms from strata in Far East Russia (Akhmetiev and Manchester 2000).

Several interesting trends can be found within subfamily Coryloidae from Paleocene to recent times including changes in nut size and bract size, symmetry, and morphology. These changes may have been related to the dispersal potential of the nutlet propagules. *Palaeocarpinus* species of Eocene age differ from Paleocene forms in bract size, shape, and type of dispersal unit (table 2). In general, Paleocene species in this genus have larger dimensions than do those in the Eocene, with the largest specimens coming from the Almont and Beccegel Creek localities. There also appears to be a shift in length : width ratio of the bract such that older forms have longer bracts while younger forms have either isodiametric bracts or those that are somewhat broader than they are long. It is also interesting that while Paleocene fruits are found both isolated and preserved within infructescences (commonly at
the Almont site), the younger species are known only from isolated winged nutlets.

In the Paleocene, the earliest fossils thought to represent Corylus nuts are considerably smaller than Eocene and extant filberts. It has been suggested that the increase in size of Corylus nuts may have been in response to coevolution with mammals (Ridley 1930; Stone 1973; Tiffney 1986) and that the ability of hazelnuts to stay afloat may also have aided in their dispersal via water transport (Stone 1973; Whitcher and Wen 2001). Other extant coryloid fruits that emerge during the Eocene and Oligocene have additional morphological innovations. For example, the asymmetry of the bracts among Carpinus fruits is present even in the earliest currently known form, C. perryae. Asymmetry may be related to the compaction of the fruits within the catkin. Another innovation, the bladder-like bracts of Ostrya fruits, thought to be elaborations for wind dispersal, is present by the Oligocene (Ridley 1930; Tiffney 1986). All of these variations suggest that, even from their initial divergence, a wide variety of adaptations for dispersal was occurring among coryloid genera in western North America.

The presence of P. barksdaleae, P. stonebergae, and P. dentatus in the Okanagan Highlands demonstrates that Palaeocarpinus extends into the Eocene in western North America as it does in Asia (Akhmetiev and Manchester 2000) and that it is coeval with the oldest record of the two extant genera. An associated pollen-bearing catkin and Corylus-like leaves also occur at Gold Mountain and Boot Hill, two Republic sites containing numerous specimens of P. barksdaleae. Together, these fossils underscore the significance of the Coryloid Betulaceae in northwestern North America during the middle Eocene. Previously known examples of Betula and Alnus from these same localities have already shown that the Betuloideae were well represented at these sites. It is now clear that both subfamilies of Betulaceae, the Betuloideae and Coryloideae, were well established and diverse in the middle Eocene of western North America.

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