

NEW DIVERSITY AMONG THE TROCHODENDRACEAE FROM THE EARLY/MIDDLE EOCENE OKANOGAN HIGHLANDS OF BRITISH COLUMBIA, CANADA, AND NORTHEASTERN WASHINGTON STATE, UNITED STATES

Kathleen B. Pigg,¹ Richard M. Dillhoff, Melanie L. DeVore, and Wesley C. Wehr²

School of Life Sciences, Arizona State University, Box 874501, Tempe, Arizona 85287-4501, U.S.A.; Evolving Earth Foundation, P.O. Box 2090, Issaquah, Washington 98027, U.S.A.; Department of Biological and Environmental Sciences, Georgia College and State University, Milledgeville, Georgia 31061, U.S.A.; and Burke Museum of Natural History and Culture, University of Washington, Box 353010, Seattle, Washington 98195-3010, U.S.A.

Newly recognized fossil infructescences and leaves of the Trochodendraceae are described from the Early/Middle Eocene McAbee and One Mile Creek sites of British Columbia, Canada, and Republic, eastern Washington State, United States. *Trochodendron drachukii* Pigg, Dillhoff, DeVore, & Wehr sp. nov., from McAbee, is an infructescence similar to that of extant *Trochodendron aralioides* Sieb. & Zucc. but strongly paniculate rather than racemose. This new species is larger and more robust than those of the Eocene flora of Republic, Washington, and has attached fruits quite similar to both extant *Trochodendron* Sieb. & Zucc. and Miocene fossils from Asia and western North America. Associated leaves are similar to those of extant *Trochodendron* except for sometimes bearing short basal auriculate extensions of the lamina. They differ from *Trochodendron nastae* Pigg, Wehr, & Ickert-Bond leaves from Republic that have palmate rather than pinnate venation. *Tetracentron hopkinsii* Pigg, Dillhoff, DeVore, & Wehr sp. nov. from One Mile Creek and *Tetracentron* sp. from Republic have leaves remarkably like those of extant *Tetracentron* Oliver, firmly establishing the presence of this genus in the Eocene. This study demonstrates that within the Trochodendraceae, a poorly understood group within the eudicot grade, both extinct forms as well as plants with quite modern-appearing fruits and leaves were present by the Eocene in northwestern North America.

Keywords: Eocene, Okanogan Highlands, *Tetracentron*, Trochodendraceae, Trochodendrales, *Trochodendron*.

Introduction

The order Trochodendrales is based on two extant genera, *Trochodendron* Sieb. & Zucc. and *Tetracentron* Oliver, that are recognized either within the family Trochodendraceae or in the separate families Trochodendraceae and Tetracentraceae (Smith 1945; Endress 1986; Doweld 1998; Endress and Igersheim 1999; Fu and Bartholomew 2001; Fu and Endress 2001). In this contribution we follow the taxonomy of the Angiosperm Phylogeny Group (APG 2003), which favors inclusion of both genera within the Trochodendraceae. Recent combined molecular and morphological analyses have failed to clarify the phylogenetic position of these taxa, although generally it has been recognized to be within the poorly resolved basal eudicot grade (Magallón et al. 1999; Judd et al. 2002; APG 2003). Early work is summarized by Smith (1945).

Trochodendron aralioides Sieb. & Zucc. is today a monotypic genus of small trees or shrubs with coriaceous, elliptical to obovate evergreen leaves that has an extant distribution restricted to areas of Japan (including the Ryukyu Islands), Taiwan, and South Korea (Smith 1945; Mabberley 1987; Fu and Endress 2001). *Tetracentron sinense* Oliver is another monotypic genus today, Asian in distribution, occurring in

Nepal, southwestern and central China, and northern Burma (Fu and Bartholomew 2001). Unlike *Trochodendron*, *Tetracentron* is characterized by thin, deciduous, actinodromous, stipulate leaves. Both genera have received considerable attention in the past because of their vesselless wood, their distinctive reproductive structures, and the difficulty in determining their taxonomic placement (Bailey and Nast 1945; Smith 1945). Both genera have racemes (and occasional panicles in *Trochodendron*) consisting of apetalous flowers. Fruits are loculicidal capsules with small, winged seeds (Smith 1945; Doweld 1998; Endress and Igersheim 1999; Fu and Endress 2001).

Although the Trochodendraceae are Asian endemics today, there is considerable fossil evidence suggesting the family had a wider distribution in the past and a long evolutionary history (Crane et al. 1990, 1991; Manchester et al. 1991; Pigg et al. 2001). The earliest evidence of leaves with “trochodendrophyll” morphology occurs in the late Albian of eastern North America. Similar forms are known throughout middle Cretaceous leaf floras of North America and Eurasia (Crabtree 1987; Upchurch and Wolfe 1987; Crane 1989). As is the case with many middle Cretaceous foliage types, these leaves have the general architecture of certain broadly defined modern groups (e.g., “platanophylls,” “protophylls,” “sapindophylls,” etc.; Crabtree 1987). However, the leaves are not assignable to modern genera, no associated fertile remains are known, and the generalized leaf types may be referable to several extant families.

¹ E-mail kpigg@asu.edu.

² Deceased April 12, 2004.

The fossil record of Trochodendraceae has been reviewed recently by Pigg et al. (2001). Late Cretaceous fossils of the extinct genus *Nordenskioldia* Heer, typically assigned to the Trochodendraceae, are known from Asia and western Canada (Vakrameev 1958; Serbet 1997). For the present contribution we accept this assignment, which has been supported by Crane (Crane 1989; Crane et al. 1991) but questioned by Doweld (1998). Wood referred to *Tetracentronites japonicus* Nishida and *T. panochetris* Page occurs in the Albian of Japan (Nishida 1962) and the latest Campanian of California (Page 1968), respectively.

Wood is also known from several Tertiary localities, including the Eocene and Oligocene of Oregon (Hergert and Phinney 1954; Scott and Wheeler 1982), the middle Tertiary of Greenland (Mathiesen 1932; Bailey and Nast 1945), and an unpublished occurrence in the Eocene Alder Lake flora of western Washington State (E. R. Strauss, written communication, 1996). Because extant *Trochodendron* and *Tetracentron* woods are quite similar, it is not clear based on wood anatomy alone whether the fossil record represents either of these extant genera or an extinct relative. *In situ* fossil pollen is known from infructescences of *Tetracentron* in the Miocene of Idaho (Manchester and Chen 2006).

Both Paleocene and Miocene floras often contain *Nordenskioldia* infructescences, which are frequently associated with *Zizyphoides* Seward & Conway leaves that have been thought to represent the same plant type (Crane et al. 1991; Manchester et al. 1991; Pigg et al. 2001). Recently, the first documented occurrence of an Eocene *Nordenskioldia* specimen from North America and the oldest evidence of the extant genus *Trochodendron* were reported from the Eocene Republic flora of Washington State (Wolfe 1989; Pigg et al. 2001). *Trochodendron nastae* Pigg, Wehr, & Ickert-Bond leaves are markedly similar to those of the extant genus except for having palmate rather than pinnate venation. Associated infructescences are in all respects similar to those of later fossil and extant examples except that they are considerably smaller. Other occurrences of *Trochodendron* infructescences and occasional leaves are all Miocene and include sites in western North America, Japan, and Kamchatka (Chelebaeva and Chigayeva 1988; Uemura 1988; Manchester et al. 1991; Fields 1996a, 1996b; Manchester 1999; Pigg et al. 2001).

Leaves assigned to the genus *Tetracentron* have been reported from several localities in North America, Russia, and Asia (Suzuki 1967; Iljinskaja 1972; Wolfe 1977; Ozaki 1987), although some of these assignments are questionable, as discussed below. The presence of *Tetracentron* in the Neogene of western North America is also documented by fruits from the Clarkia flora, in north central Idaho (Manchester and Chen 2006).

In this study, we describe newly recognized fossil representatives of the Trochodendraceae from localities within the Okanogan Highlands of British Columbia and eastern Washington State. *Trochodendron drachukii* Pigg, Dillhoff, DeVore, & Wehr sp. nov. is based on a robust infructescence from the McAbee site in south central British Columbia, Canada. Leaves associated with *T. drachukii* that resemble extant *Trochodendron* are also described. *Tetracentron hopkinsii* Pigg, Dillhoff, DeVore, & Wehr sp. nov. is described from well-preserved leaves from One Mile Creek near Princeton, British Columbia, and *Tetracentron* sp. from Republic, Washington, United States. Together with the previously recognized ele-

ments from Republic, this material demonstrates that the Trochodendraceae were undergoing considerable diversification during the Early-Middle Eocene in northwestern North America.

Material and Methods

The localities from which the present material is described are part of the Okanogan (“Okanagan” in the alternative Canadian spelling) Highlands flora that extends from central British Columbia into northeastern Washington State (fig. 1). During the Early and Middle Eocene, a series of faults created northwest-trending grabens and half grabens in the southern Canadian Cordillera (Ewing 1980, 1981; Mathews 1991). At the same time, a volcanic arc contributed vast amounts of sediments that infilled these basins. The combination of numerous basins and abundant, rapidly deposited sediments created circumstances ideal for preserving a rich regional record of flora and fish and insect faunas in a series of lacustrine shale deposits.

Radiometric dating for the localities used in this study ranges from Early Eocene to Middle Eocene. The McAbee locality, near Cache Creek, British Columbia, is located at 50°47.181'N, 121°08.568'W (Manchester and Dillhoff 2004). This site contains a rich assemblage of leaf and fruit megafossil compressions documenting a diverse temperate flora consisting of at least 100 taxa. The McAbee conifer flora is dominated by many members of the Pinaceae and Cupressaceae *sensu lato* but also includes at least one member of Taxaceae and two species of *Ginkgo* L. *Ulmus* L., *Fagus* L., *Betula* L., and *Alnus* L. dominate the angiosperm fossil record, but rarer specimens reveal the diversity of the flora (Dillhoff et al. 2001, 2005). The McAbee locality has recently provided the earliest known occurrence of *Fagus* based on fruits and seeds (Manchester and Dillhoff 2004). The matrix containing fossils has been interpreted as an altered diatomite (Mustoe 2005), confirming

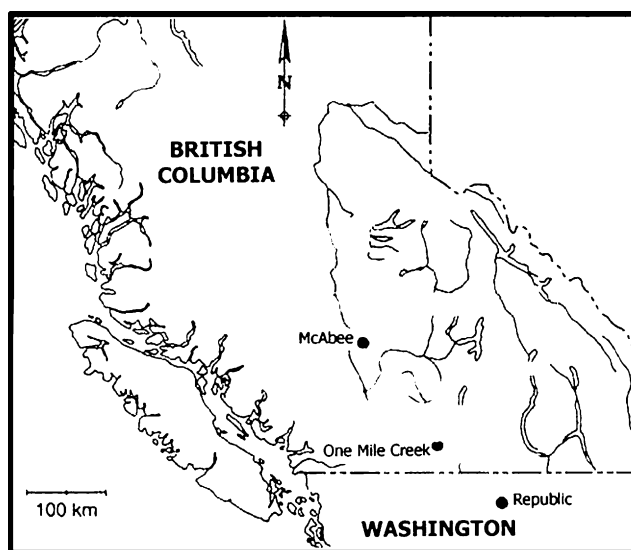


Fig. 1 Map of Okanogan Highlands, British Columbia, Canada, and northeastern Washington State, United States, indicating collecting localities.

that the depositional environment was lacustrine (Manchester and Dillhoff 2004).

The One Mile Creek locality (also known as Allison Creek) occurs in the Allenby Formation of southern British Columbia (Crane and Stockey 1987) 8 km north of Princeton, on the Princeton-Merritt Highway 5, approximately at the confluence of One Mile Creek and Summers Creek (universal transverse Mercator grid: UN 226940, 49°31.936'N, 120°31.375'W). Fossils are preserved as compressions in a finely laminated light green gray shale typical of lacustrine deposits. In general, the One Mile Creek flora is less diverse than fossil assemblages from other Okanagon Highlands sites, containing ca. 36 genera of temperate hardwood and conifer trees. The dominant taxon present is *Betula leopoldae* Wolfe & Wehr (Crane and Stockey 1987), and conifers are represented only by Pinaceae and Taxodiaceae. The recently described species *Ulmus okanaganensis* Denk & Dillhoff (Denk and Dillhoff 2005) was first found with leaves and fruits in attachment here (Manchester 1989). Other genera of note include *Tsukada davidifolia* Wolfe & Wehr (Wolfe and Wehr 1987), numerous species of *Acer* L. fruits and leaves (Wolfe and Tanai 1987), and a diverse assemblage of rosaceous leaf forms representing both extinct and extant genera (Wolfe and Wehr 1988; DeVore et al. 2004; DeVore and Pigg, forthcoming).

The Republic flora of eastern Washington is the most highly diverse and most completely studied of the Okanagon Highland floras to date. Details about this flora have been summarized previously and are still forthcoming (e.g., Wolfe and Wehr 1987; Pigg et al. 2001; Greenwood et al. 2005). While this microthermal assemblage was initially described as mixed conifer (Wolfe and Wehr 1987), more recent studies have indicated a high angiosperm diversity (Greenwood et al. 2005). Among the significant groups represented are the maples (Wolfe and Tanai 1987), Betulaceae (Pigg et al. 2003), and especially the Rosaceae (DeVore and Pigg, forthcoming).

Specimens were photographed and scanned digitally for illustrations using Adobe Photoshop 7.0. Leaf morphology terminology follows that of the Leaf Architecture Working Group (1999). Extant specimens of *Trochodendron* and *Tetracentron* were collected at the Washington Arboretum, Seattle, and studied from University of Washington (WTU) and Arizona State University (ASU) herbarium sheets. Specimens are deposited at the Burke Museum of Natural History and Culture, University of Washington, Seattle (UWBM), the Stonerose Interpretive Center, Republic (SR), and the Thompson Rivers University, Kamloops, British Columbia, Canada (UCCIPRL).

Systematics and Descriptions

Family—Trochodendraceae

Genus—*Trochodendron* von Siebold & Zuccarini 1838

Type species—*Trochodendron aralioides* Sieb. & Zucc.

Species—*Trochodendron drachukii* Pigg, Dillhoff, DeVore, & Wehr sp. nov. (Fig. 2A, 2B, 2D)

Species diagnosis. Infructescence paniculate, with several peduncles, each branched repeatedly and bearing a combina-

tion of basal peduncles twice branched and apical peduncles bearing single fruits; fruits 3–4 mm long × 3–4 mm wide with six or more fused carpels; styles persistent, curved, up to 2 mm long.

Holotype. UWBM 97819 (fig. 2A, 2B, 2D). The specimen is housed in the Burke Museum of Natural History and Culture, University of Washington, Seattle.

Type locality. McAbee near Cache Creek, British Columbia (Manchester and Dillhoff 2004).

Age and stratigraphy. Early Eocene unnamed formation of the Early to Middle Eocene Kamloops Group.

Etymology. The specific epithet *drachukii* is named in honor of Robert Drachuk, Delta, Utah, who found important specimens used in this diagnosis.

Description. *Trochodendron drachukii* is based on a single specimen of a well-preserved paniculate infructescence 11.4 cm long containing 23 observable attached fruits from McAbee (fig. 2A, 2B, 2D; fig. 3A). The infructescence has a woody axis with a basal diameter of 2 mm and is similar in general appearance to extant *T. aralioides* and related Miocene fossils (fig. 2C, 2E; fig. 3). It is organized into a panicle with four basal three-times-branched peduncles, each peduncle terminating in a fruit and bearing two alternately attached subtending pedicellate fruits (fig. 2A, 2D; fig. 3A), and 11 apical peduncles bearing single fruits (fig. 2A, 2B). The primary peduncles of the compound peduncles are 1.0–2.4 cm long with their lengths decreasing apically; secondary peduncles are 3–6 mm long. Individual fruits are 3–4 mm long × 3–4 mm wide and consist of six or more fused carpels (fig. 2B, 2D). They range in outline depending on the angle of compression but appear generally triangular with an acute base and a broader, truncate apex. The fruits are striated vertically, and many of them have well-preserved persistent styles up to 2 mm long that curve outward from their points of attachment (fig. 2B, 2D). The nectary disks that characterize extant fruits of *Trochodendron* were not observed.

Associated Trochodendron-like Leaves

A distinctive *Trochodendron*-like leaf type has been discovered in the same deposit with the infructescence of *T. drachukii*. This description is based on two isolated complete leaves and a branch bearing six observable leaves in attachment. Leaves are borne alternately on the branch on stout petioles that are 8–11 mm long × 2 mm thick (fig. 4A). The lamina of each leaf is elliptic and typically symmetrical and 10.0–12.7 cm long × 3.0–3.9 cm wide, with L : W ratio of 3.3 : 1 (fig. 4A, 4D, 4E). The leaf apex is acuminate, and the leaf base is convex and slightly asymmetric. Lateral to the leaf base and distinct from it, most of the specimens have paired basal extensions of the lamina (“coattails”) that extend at 60° from the side of the leaf. These structures are up to 6 mm long, pointed, and 1.5 mm at their widest point (fig. 4A, 4B, 4E).

The leaf margin is serrate for the apical seven-eighths of the leaf with the basal one-eighth of the margin entire; one or two teeth occur per centimeter, decreasing basally in number and size (fig. 4F). The primary vein is strong, distinct, and up to 2 mm wide basally, and it extends to the leaf apex, smoothly decreasing in thickness apically to 0.2 mm (fig. 4C, 4D).

The secondary venation is pinnate and brochidodromous (fig. 4C). Ten to 12 pairs of secondary vein pairs arise decurrently

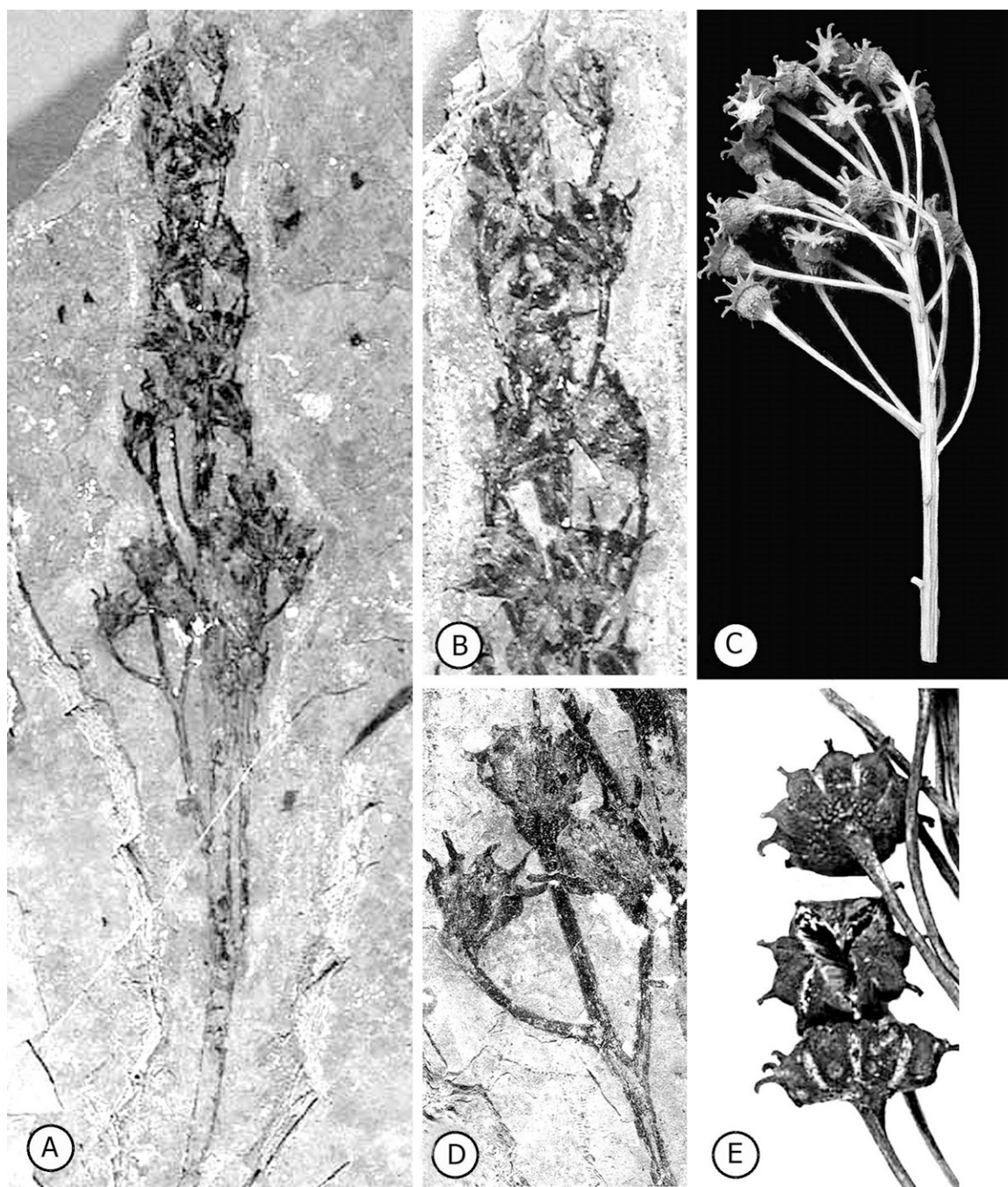


Fig. 2 *Trochodendron drachukii* sp. nov. infructescence (A, B, D) and extant *Trochodendron aralioides* fruits and infructescence (C, E). A, Complete infructescence of holotype showing panicle organization, UWBM 97819, $\times 1.5$. B, Higher magnification of A, showing detail of individual fruits, UWBM 97819, $\times 2.7$. C, Extant infructescence, to show racemose organization, $\times 1.2$. D, Higher magnification of A, showing panicle, UWBM 97819, $\times 3.2$. E, Portion of extant infructescence, for comparison of fruits, $\times 3.5$.

from the primary vein initially at angles of ca. 32° basally, decreasing to ca. 23° apically. Secondary veins are initially straight at their point of divergence from primaries; then they typically curve inward apically. Weak intersecondaries occur between secondary veins and branch out laterally to form brochidodromous loops (fig. 4C). A marginal vein that parallels the outer edge of the leaf is visible in some basal areas (fig. 4F). Tertiary

veins diverge at angles of 125° – 150° and are mixed percurrent, opposite to alternate, straight to sinuous, and spaced 2–6 mm apart (fig. 4C, 4F). Quaternary veins are opposite percurrent. Fifth-order veins have not been observed.

Marginal teeth are concave apical, are convex to straight basal *sensu* Leaf Architecture Working Group (1999), and typically have a glandular apex (fig. 4F). Teeth are vascularized by

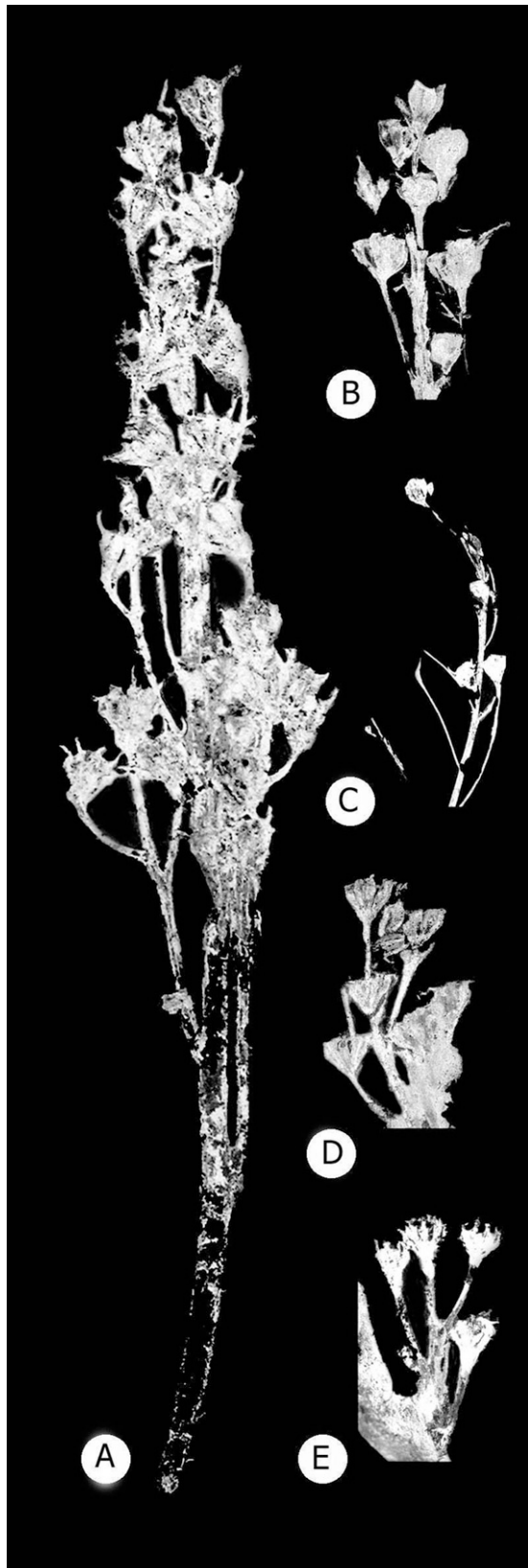


Fig. 3 Associated *Trochodendron drachukii* infructescence from McAbee in comparison to other fossil forms. A, *T. drachukii* holotype, redrawn from UWBM 97819, $\times 1.6$. B, Emerald Creek (Miocene, ID), redrawn from Fields (1996a), $\times 0.8$. C, Succor Creek (Miocene, OR and ID), redrawn from Manchester et al. (1991, fig. 29), $\times 0.5$. D, Kamchatka (Miocene), redrawn from specimen, $\times 0.8$. E, Japan (Miocene), redrawn from Manchester et al. (1991, fig. 30), $\times 0.5$.

a single vein that enters toward the apical area, and the sinuses between teeth are characteristically rounded (fig. 4F).

Genus—*Tetracentron* Oliver

Type species—*Tetracentron sinensis* Oliver

Species—*Tetracentron hopkinsii* Pigg, Dillhoff, DeVore, & Wehr sp. nov.

Species diagnosis. Leaves up to 9.5 cm long \times 7.5 cm wide, L : W ratio 1.3 : 1; petiole 4.3 cm long \times 2 mm wide, broadening to 5 mm wide at base; lamina elliptical, base cordate. Primary venation actinodromous, petiole robust, midvein thin, straight throughout most of length; two or three pairs of lateral primaries; outermost lateral primaries thin, 90° to midrib, inner one-to-two pairs of primary veins strong; secondaries, tertiaries, and quaternaries alternate/percurrent. Marginal teeth present, regular along margin except for basalmost region; well developed; straight to convex apical, convex basal *sensu* Leaf Architecture Working Group (1999), $3\text{--}5\text{ cm}^{-1}$, at ca. 1.5-mm intervals, 1.5–4 mm long; teeth with persistent apical foliar glands.

Holotype. UWBM 54185 (fig. 5A), Burke Museum of Natural History and Culture, University of Washington, Seattle.

Paratype. UWBM 56700ab (fig. 5B, 5D–5G), Burke Museum of Natural History and Culture, University of Washington, Seattle.

Type locality. One Mile Creek.

Age and stratigraphy. Allenby Formation, Early/Middle Eocene.

Etymology. This species is named for Donald Q. Hopkins, Middleton, Vermont, in recognition of his concerted collecting efforts and numerous discoveries at One Mile Creek and many other Okanogan Highlands sites.

Description. This description is based on two specimens of well-preserved leaves, the holotype, an individual leaf showing ca. two-thirds of the specimen and lacking the apex (fig. 5A), and the paratype, a part-counterpart specimen showing most of the leaf, including the apex, yet lacking the base (fig. 5B, 5D–5G). Together, these two specimens resemble extant leaves of *Tetracentron* remarkably (fig. 5C, 5H). The first specimen is fragmentary but preserved for 5.2 cm of its length and has a complete width of 7.2 cm (fig. 5A). The second is 9.3 cm long and preserved for 5 cm of its width (fig. 5B, 5E). Based on estimates from reconstructing the part-counterpart specimen and comparison with comparable extant leaves of similar dimensions (fig. 5C), the fossils are estimated to be ca. 9.5 cm long \times 7.5 cm wide. L : W ratio is 1.3 : 1. The petiole is complete on the first leaf, 4.3 cm long and around 2 mm wide, broadening at the base at the attachment point to 5 mm with a flat lower surface (fig. 5A). Leaves are elliptical and have a cordate base (fig. 5A) and, as seen in the paratype, with a slight, acuminate apex (fig. 5B,

redrawn from Fields (1996a), $\times 0.8$. C, Succor Creek (Miocene, OR and ID), redrawn from Manchester et al. (1991, fig. 29), $\times 0.5$. D, Kamchatka (Miocene), redrawn from specimen, $\times 0.8$. E, Japan (Miocene), redrawn from Manchester et al. (1991, fig. 30), $\times 0.5$.

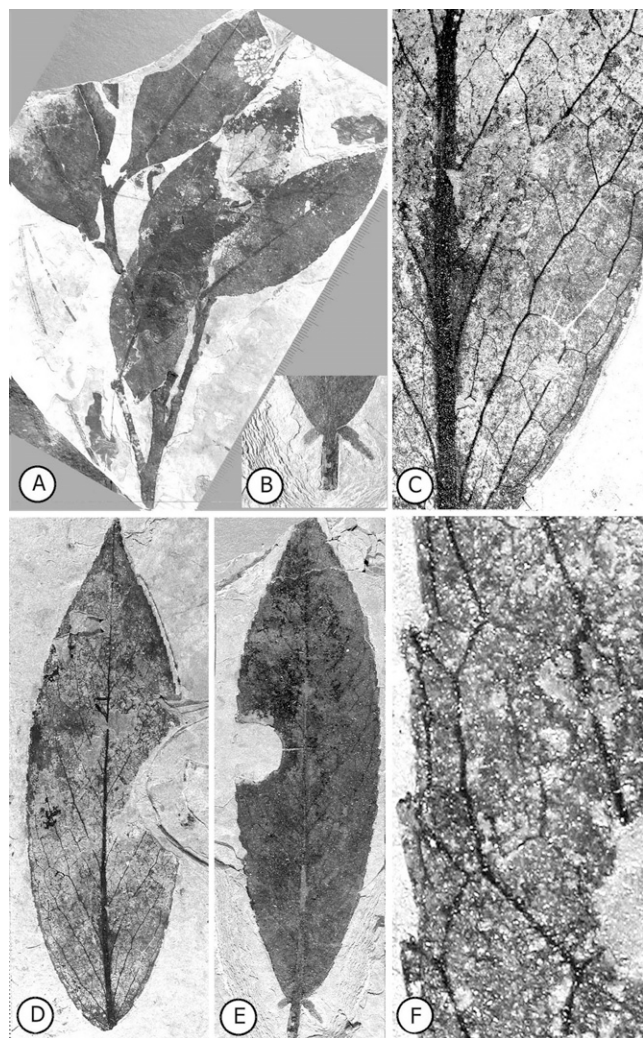


Fig. 4 *Trochodendron* leaves associated with *Trochodendron drachukii* at McAbee. **A**, Cluster of leaves attached to stem. Note short petioles and basal auriculate extensions of lamina, UCCIPRL 15F428, $\times 0.4$. **B**, Detail of leaf base illustrated in **E**, showing basal auriculate extensions of lamina, UWBM 97821, $\times 10$. **C**, Detail of leaf venation illustrated in **D**. Note secondary pinnate venation, weak intersecondaries, and marginal vein, UWBM 97822, $\times 17$. **D**, Almost complete lamina. Note attenuate apex, prominent midrib basally thinning toward apex; attenuate apex and acute, oblique base, UWBM 97822, $\times 0.5$. **E**, Leaf showing basal extensions of lamina, thick petiole, and circular damage pattern (left), UWBM 97821, $\times 0.5$. **F**, Detail of leaf margin, showing teeth and their vascularization, brochidodromous loops, and marginal vein, UWBM 97820, $\times 15$.

5E). The margin is serrate, with well-developed teeth for the complete length of the leaf (fig. 5A, 5B, 5E).

Primary venation is actinodromous (fig. 5A) with two to three pairs of lateral primaries. The petiole is robust (fig. 5A). In comparison, the midvein is fairly thin and straight in its course, extending almost to the apex, where it undulates and forks (fig. 5B). The outermost pair of lateral primaries are thin and extend out laterally at 90° to the midrib (fig. 5A); the inner one or two pairs are more vertically aligned (fig. 5A). The innermost lateral primaries are strong and produce

ca. six pairs of secondary veins. Outer lateral primaries are somewhat thinner. Secondary veins are thin and diverge from the midvein at an angle of 32° – 40° to the midvein. They join admedial secondaries from the inner lateral primaries to form a chevron bracing in the median part of the leaf (fig. 5A, 5B, 5G). Tertiary veins diverge at an angle of 60° – 70° and are alternate percurrent. Quaternary veins are also alternate percurrent, and fifth-order venation is not preserved.

Teeth are regularly spaced at ca. 1.5-mm intervals with three to five occurring per centimeter (fig. 5A, 5B, 5E, 5G). They are mostly straight apical and convex basal *sensu* Leaf Architecture Working Group (1999), but they vary near the apex, where they may fork (fig. 5B, 5E). Venation of the tooth is composed of a single midvein and two lateral veins that converge into a persistent laminar gland (fig. 5D, 5E, 5G), similar to those of extant *Tetracentron* (fig. 5H).

Tetracentron sp. from Republic

As we were completing this article, we discovered an additional *Tetracentron* leaf from Republic, Washington (fig. 6). Because this leaf varies somewhat from *Tetracentron hopkinsii* and cannot be compared in all details because of limits in preservation, we are describing it as *Tetracentron* sp.

The leaf is 9.3 cm long \times 8.6 cm wide at the widest area, resulting in a L : W ratio of 1.9 : 1. This specimen is obovate with a slightly asymmetric cordate base and an incomplete but apparently acuminate apex, given the taper of the preserved apical area (fig. 6A). A petiole is not preserved. Primary venation is similar to that of *T. hopkinsii* and extant *Tetracentron sinense*, with a major vein surrounded by a prominent inner pair of lateral primaries that run almost parallel to the midvein and at least one thinner, more broadly arched pair of outer lateral primaries (fig. 6A). The midvein produces at least four pairs of alternately arranged secondaries that become more crowded toward the apex. Lateral primaries produce secondaries, but preservation limits a complete description. Higher-order venation is only sporadically preserved.

The leaf margin is fragmented, although part of it is fairly well preserved and shows fairly regular teeth at a concentration of 4 cm^{-1} (fig. 6D). Like those of *T. hopkinsii*, individual teeth are rounded and straight to concave apical, convex basal *sensu* Leaf Architecture Working Group (1999) and have evidence of a persistent, terminal gland (fig. 6B, 6C). They are vascularized by a single median vein that persists to the apex and associated lateral veins.

Discussion

Further Diversity in Fossil Trochodendraceae

Circumscribing two new taxa within the Trochodendraceae adds to our knowledge of the family's distribution and diversity during the Eocene. A glimpse of the variation within Trochodendraceae is starting to emerge. *Trochodendron drachukii* is considerably larger and more robust than the infructescences described from the Eocene Republic locality in association with leaves of *Trochodendron nastae* (Pigg et al. 2001). In comparison with other known fossil and extant *Trochodendron* species, they are most similar in size to the Miocene forms (fig. 3B, Clarkia; fig. 2D, Succor Creek; fig.

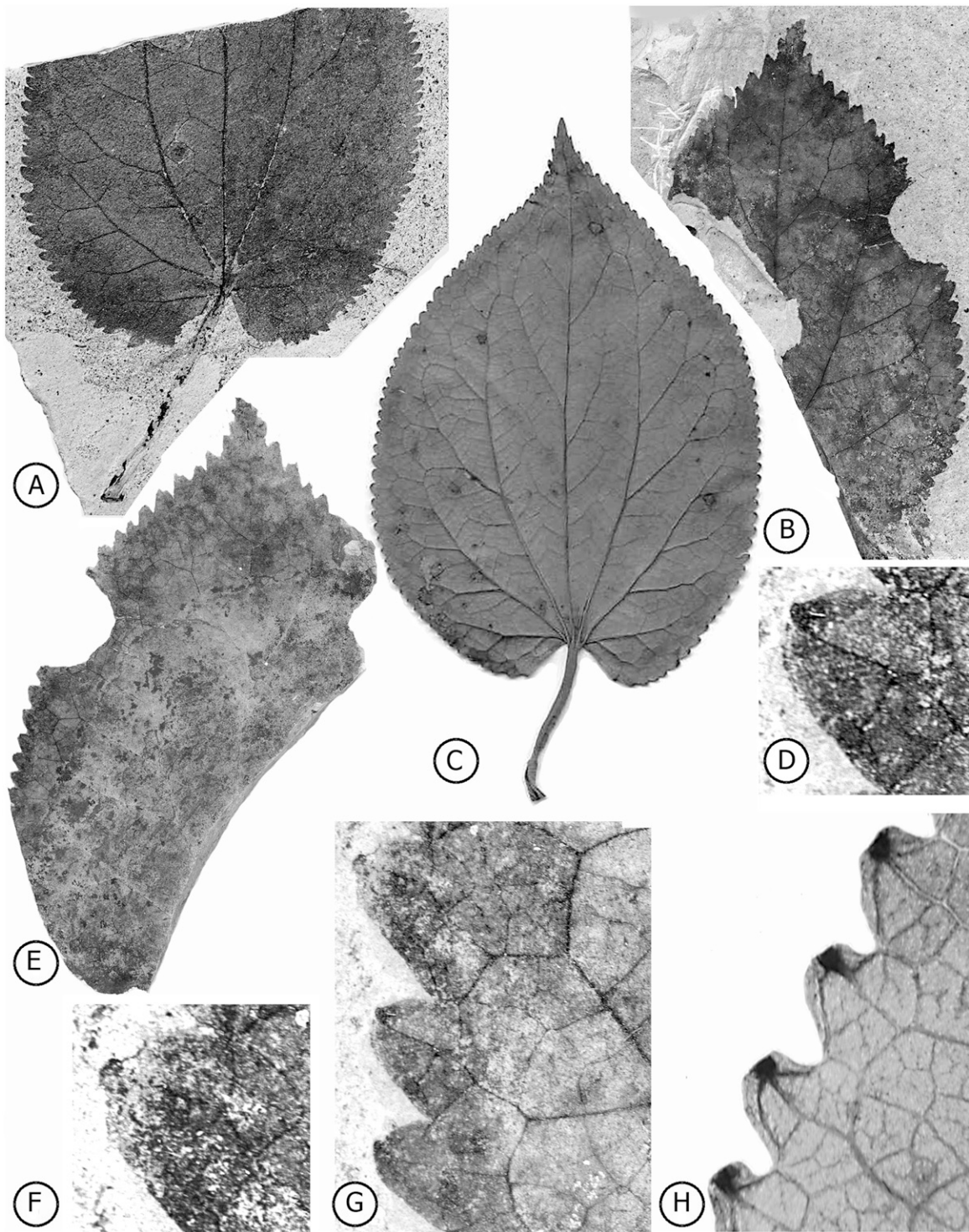


Fig. 5 *Tetracentron hopkinsii* sp. nov. (A, B, D–G) and extant *Tetracentron sinense* (C, H). A, Holotype showing basal portion of leaf. Note prominent cordate base, palmate venation, and serrate margin with well-developed teeth, UWBM 54185, $\times 0.9$. B, Paratype specimen (counterpart of E), showing slightly acuminate leaf apex, venation, and well-developed marginal teeth. Note prominent insect damage (right), UWBM 56700a, $\times 0.8$. C, Extant leaf for comparison, $\times 0.9$. D, Higher magnification of E showing detail of the major vein entering a marginal tooth, and a persistent apical gland, UWBM 56700b, $\times 12$. E, Paratype specimen (counterpart of B), showing leaf and margin shape, apex, and insect damage (left), UWBM 56700b, $\times 1$. F, Higher magnification of E, showing detail of central and two lateral veins to tooth, UWBM 56700b, $\times 12$. G, Higher magnification of E, showing marginal venation and teeth with persistent glands, UWBM 56700b, $\times 8$. H, Higher magnification of extant leaf margin to show characteristic venation and persistent apical glands, $\times 7.5$.

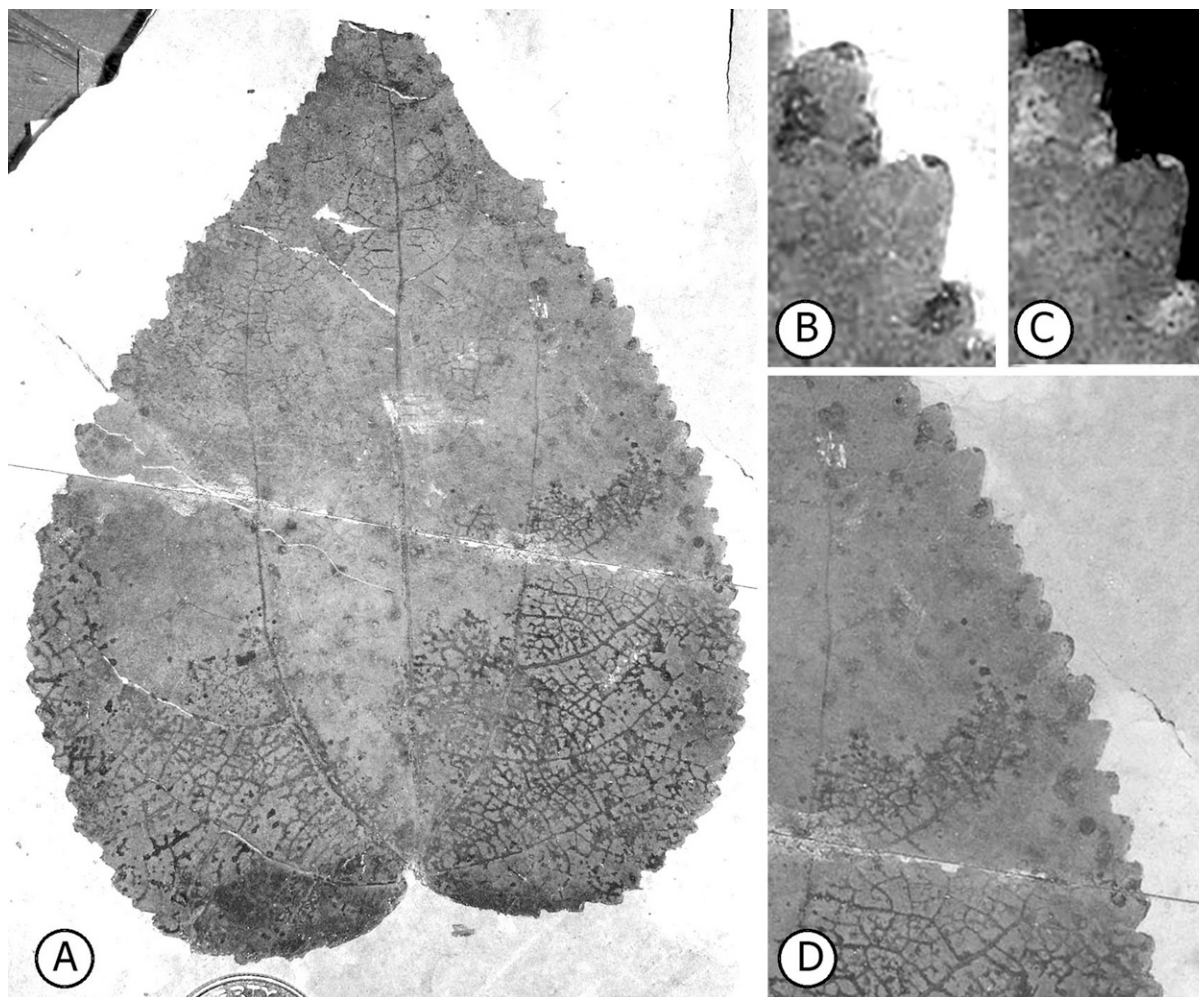


Fig. 6 *Tetracentron* sp. from Republic. A, Overview of specimen, showing shape, cordate base, attenuated apical region, and marginal teeth (right), SR 97-05-11, $\times 1.2$. B, Detail of leaf margin, showing evidence of rounded glandular teeth with straight to concave apical, convex basal shape and single vein entering tooth, and two lateral subsidiaries, SR 97-05-11, $\times 6.6$. C, Inverted image of B, showing detail of venation, SR 97-05-11, $\times 6.6$. D, Margin, showing several well-preserved teeth and some areas of higher order venation, SR 97-05-11, $\times 1.8$.

2E, Kamchatka) and the extant forms (fig. 2C, 2E). Like other fossils, they are generally similar to the extant fruits, but stamen structure and the nectaries known from extant fruits were not preserved. The infructescence architecture of the McAbee specimen is paniculate rather than the more typical racemes of modern species, although panicles do occasionally occur in extant *Trochodendron aralioides*. Paniculate forms have been recorded in the *Flora of China* (Fu and Endress 2001) and seen recently by two of us (K. Pigg and M. DeVore, personal observation, 2004) in the Royal Botanic Gardens at Edinburgh, Scotland.

Leaves associated with *T. drachukii* have pinnate venation like that in the later Miocene fossils *Trochodendron evense* from Kamchatka, *Trochodendron protoaralioides* from Japan, and the extant species *T. aralioides*. This is in contrast to the only previously known Eocene *Trochodendron* leaf type, *T. nastae* from Republic, which has palmate venation (Pigg et al. 2001). Leaves associated with *T. drachukii* have a very strong midrib that thins apically, a less prominent chev-

ron pattern than that typical of other *Trochodendron* leaves, relatively short petioles, and a pair of basal auriculate extensions not seen in other species. These leaves are on the large side of the size range when compared to extant *T. aralioides*, and they are larger than those of *T. nastae*, previously described from Republic (Pigg et al. 2001).

Tetracentron hopkinsii from One Mile Creek and *Tetracentron* sp. from Republic are quite similar to one another and may be assignable to the same species. However, since we have only a single incomplete specimen from Republic, we are not assigning it to *T. hopkinsii* at present. While details of venation and margin compare favorably to those of *T. hopkinsii*, this leaf differs in overall shape, with a much broader lamina toward the base, while *T. hopkinsii* is more elliptical (fig. 5A, 5B, 5E; fig. 6A). These two Eocene forms are both remarkably similar to extant *Tetracentron sinense* (table 1). They share the extant form's general shape, cordate base, and acute to acuminate apex, and they have the same venation architecture of a stout midrib with two or three

Table 1
Morphological Details of *Tetracentron* Leaves

Taxon	<i>T. hopkinsii</i> ^a	<i>T. sp.</i> ^a	<i>T. ibei</i> ^b	<i>T. masuzawaense</i> ^c	<i>T. sp.</i> ^c	<i>T. sinense</i> ^{a,b,c,d}
Age occurrence	Eocene British Columbia	Eocene Washington	Mio-Pliocene Japan	Late Miocene Japan	Late Pliocene Japan	Extant, central and sw China, Himalayas
Size (L × W cm)	9.5 × 7.5	9.3 × 8.6	7.3–8.2 × 5.7	5.8–13.5 (10) ^e × 4.5–9 (6.3) ^e	10–12 × 6–7	6–10 × 4.2–8.4, ^d 9.4–9.8 × 6.7–7.1 ^a
L : W ratio	1.3 : 1	1.9 : 1	1.21 : 1	1.3–1.9 : 1 (1.5 : 1)	1.6–1.7 : 1	1.2–1.6 : 1, ^d 1.4 : 1 ^a
Lamina shape	Ovate	Ovate	Ovate, slightly asymmetric	Cordate ^c (to elliptical) ^a	Cordate	Ovate to elliptical
Broadest area	Central portion	Basal 1/4	1/3 from base	Central portion	...	Central portion to lower 1/3
Base	Cordate	Cordate, asymmetric	Shallowly to deeply cordate	Shallowly to deeply cordate	Cordate	Truncate to shallowly cordate ^b
Apex	Slightly acuminate	Incomplete but acuminate	Acuminate	Caudate-acuminate 1.5–2.5	Caudate-acuminate	Acute ^b to acuminate ^a
Petiole (L × W cm)	Robust, 4.3 × .2, .5 basally	...	1 × .13	Thick, 1.5–3 × .02–.03	...	Cannelized, thick, with stipules
Midvein	Thin, + / – straight apical undulating and branching	Thin, straight	Straight	Stout, nearly straight	Straight, sinuous near apex	Thin, fairly straight
Pairs of lateral primaries	2–3	2	3	2, rarely 3	2	3 usually, up to 4
Overall tooth shape	Rounded	Rounded	Slenderly triangular ^b	Slenderly triangular ^b	Slenderly triangular ^b	Rounded to slenderly triangular ^b
Tooth shape apical	Straight to concave	Straight to concave	Concave	Concave to straight	...	Straight to concave
Tooth shape basal	Convex	Convex	Convex	Convex	...	Convex
Teeth per cm ⁻²	3–5	4	5	2.0	...	5–7
Intervals between teeth (cm)	1.5	1.5	1	1.5–2.7	...	1.5–2
Tooth length (mm)	1.5–4	1.7–2.9	5.0	1.58–1.0

^a Present study.

^b Suzuki (1967).

^c Ozaki (1987).

^d Bailey and Nast (1945).

^e Average as cited from Ozaki (1987).

pairs of lateral primaries. The leaf margin in all of these forms is serrate with very regular rounded teeth along all but the basalmost margins. Teeth are most often straight (and occasionally concave) apical and convex basal *sensu* Leaf Architecture Working Group (1999). Only slight differences between the Eocene and extant leaves are observed. Modern *Tetracentron* can have slender triangular teeth that have not been observed in the fossil, and the fossil forms tend to have less densely spaced teeth (ca. 3–5 cm⁻¹ in contrast to 5–7 cm⁻¹).

The newly discovered *Tetracentron* sp. from the Republic flora confirms the presence of this genus at two Okanogan Highlands localities. These specimens document the best evidence to date for an Eocene occurrence of the genus in North America. It is further intriguing that both *Tetracentron* and *Trochodendron nastae* occur together at Republic, given the separate distributions of these two genera in Asia today (Pigg et al. 2001).

Previous reports of fossil *Tetracentron* leaves have been reviewed by Ozaki (1987). Based on our review of the literature, we accept the Japanese occurrences as good examples of *Tetracentron*, including *Tetracentron ibei* Suzuki (Suzuki

1967), the specimens assigned by Tanai (1981) to *Tetracentron piperoides* (Lesquereux) Wolfe, and *Tetracentron masuzawaense* (Murai) Ozaki and *Tetracentron* sp. (Ozaki 1987). In our opinion, the material from Alaska described as *T. piperoides* by Wolfe (1977) does not show the critical details necessary to confidently place it in the genus *Tetracentron*. At the time Wolfe described this species, which was perhaps the first report of *Tetracentron* leaves in North America, he did not have the wider range of fossil material that exists today to fully and clearly delimit the genus. The broadly spaced teeth and general shape of the leaves are somewhat more reminiscent of *Zizyphoides* specimens we have seen in the Okanogan Highlands floras. In contrast, Japanese fossil leaves are quite similar to our material and to extant *Tetracentron*. They are of similar dimension and organization as *Tetracentron hopkinsii* and *Tetracentron* sp. from Republic (table 1). They have more extremely acuminate apices but are within the range of variation seen in extant forms (K. Pigg, personal observation). The one distinguishing feature that seems to set these leaves apart from both extant and Eocene forms is the

length and shape of their teeth, which are “slenderly triangular” (Ozaki 1987) rather than rounded.

Considerable confusion has surrounded Tertiary fossil leaves of three types: (1) the *Tetracentron* type, (2) the *Cercidiphyllum* type, and (3) the *Zizyphoides* type. Taxonomic features of extant *Tetracentron* have been previously reviewed by Bailey and Nast (1945) and Wolfe (1989), while fossil *Tetracentron* leaves that we accept have been reviewed by Tanai (1981) and Ozaki (1987). Extant *Cercidiphyllum* and the closely related fossil forms referred to *Cercidiphyllum* and *Joffrea* have been discussed in detail from Paleocene sites by Tanai (1981), Crane and Stockey (1985), and Crane et al. (1990). Leaves of *Zizyphoides* that are thought to be the leaves of the *Nordenskioldia* plant have been described from the Paleocene and Miocene, particularly of western North America (Crane et al. 1990, 1991; Manchester et al. 1991). Although Eocene leaves of this type have not been reviewed in similar detail, they are relatively common components of the Okanogan Highlands floras (K. B. Pigg, R. M. Dillhoff, M. L. DeVore, and W. C. Wehr, personal observations, 2002).

All three of these leaf types have a common bauplan. All are actinodromous with two to three pairs of lateral primary veins, and all share similar higher-level venation features. Some authors have attempted to separate the genera on slight variations in these details, but they are essentially the same, and variation within these characters and taxonomic assignment does not appear to be correlated. In our opinion, some leaves previously assigned to *Tetracentron* more closely resemble *Zizyphoides*, *Cercidiphyllum*, or a variety of other genera. For example, two of the three leaves described by Wolfe (1977, plate 5, fig. 4; plate 22, fig. 3) have the characteristic irregular

lobes that are similar to those seen in *Zizyphoides* (Crane et al. 1991; Manchester et al. 1991). The third leaf (Wolfe 1977, plate 28, fig. 7) is indeterminate. In their reconstruction of the “*Joffrea*” plant, which produces leaves very similar to those of extant *Cercidiphyllum*, Crane and Stockey (1985) state that the leaves typically lack petioles and note, in fact, that only a single specimen shows a complete petiole. Note, however, that this figure and a second leaf (Crane and Stockey 1985, figs. 58, 62) show either shallow undulations or irregularly lobed margins typical of *Zizyphoides*, rather than the even, regular margins seen in typical *Joffrea* leaves (Crane and Stockey 1985, figs. 56, 63, 64) or those of extant *Cercidiphyllum* (Crane and Stockey 1985, fig. 86).

Several features can be used to consistently separate *Tetracentron*, *Cercidiphyllum*, and the closely related *Joffrea* leaf. These include (1) leaf shape, (2) leaf base, (3) leaf apex, and (4) features of the glandular teeth, including their persistence and venation (table 2). (1) *Cercidiphyllum* and *Joffrea* leaves are typically almost round with a L : W ratio approaching or equal to 1 : 1. In contrast, leaves of *Tetracentron* tend to be longer (ca. 1.5 : 1 L : W ratio). (2) In *Cercidiphyllum* the leaf base is variable, shallow, rarely slightly cordate, but in *Tetracentron* leaves have typically deeply, sometimes shallowly cordate bases, but rarely other types of morphologies. (3) In *Cercidiphyllum* the leaf apex is blunt and rounded, while in *Tetracentron* it is often highly acuminate. (4) *Cercidiphyllum* leaves have teeth that are symmetric and rounded, and the gland is typically torn out in mature leaves, leaving a small hole. One major vein enters the center of the tooth, and small marginal veins connecting adjacent gland tips are lacking. In *Tetracentron* the apical glands on teeth are more

Table 2

Comparison of Leaf Morphological Features of *Tetracentron*, *Zizyphoides*, and *Joffrea* Leaves

	<i>Tetracentron</i> ^{a,c}	<i>Zizyphoides</i> ^b	<i>Joffrea</i> ^c	<i>Cercidiphyllum</i> ^{b,d}
Occurrence	Extant	Eocene	Eocene	Extant
Petiole	Stout and cannelized; stipulate	Usually very long and thin	Usually short to long	Medium, up to 1/2 length of lamina
Lamina shape	Ovate	Round to ovate	Round to deltoid	Round to ovate or elliptic
L : W	1.2–1.9 : 1	1 : 1–1.2 : 1	Ca. 1 : 1	.9–1.4 : 1 (avg. 1.17 : 1)
Base	Truncate to highly cordate	Truncate to oblique	Truncate to cordate	Truncate to cordate
Apex	Acuminate, sometimes extremely so	Rounded, variable	Rounded	Rounded to convex
Teeth	Uniform serrate, equal size	Irregular lobes to broad teeth, variable size	Uniform serrate	Uniform serrate
Tooth shape	Straight to concave apical; convex basal	Usually convex, sometimes straight apical; convex basal	Straight apical; straight basal	Convex apical; convex basal
Glands on teeth	Present, persistent	Occasional but not prominent	On young leaves, torn on mature leaves	This study
Tooth venation	1 major and 2 subsidiary veins; marginal vein joins adjacent teeth	Major vein typically asymmetric, no subsidiaries; often curved, marginal vein may join adjacent teeth	1 central and 2 lateral veins, all of similar thickness; no joining marginal vein	1 central and 2 lateral veins, all of similar thickness; no joining marginal vein

^a Data taken from Bailey and Nast (1945).

^b R. Dillhoff, unpublished data.

^c Crane and Stockey (1985).

^d Tanai (1981).

^e This study.

persistent in mature foliage and are laced together with a single major vein entering the center of the gland and two small adjacent marginal veins extending to the sinuses (fig. 5D, 5F–5H).

Zizyphoides leaves can be separated from these types as well. *Zizyphoides* leaves have the widest range of morphological variation, particularly in leaf shape. They may be very round like *Cercidiphyllum*, but they are often elliptical and occasionally obovate. They can be distinguished from the other genera by the leaf margin ranging from gentle undulations to deep irregular lobes rather than the regular, smaller serrate teeth seen in *Cercidiphyllum*, *Joffrea*, and *Tetracentron*. *Zizyphoides* leaves have been described from Paleocene (Crane et al. 1991) and Miocene (Manchester et al. 1991) strata in western North America and are well represented in the Eocene Okanogan Highlands floras. The range of variability of the Eocene forms has yet to be fully detailed. With further study it may be possible to better interpret the full range of variability between *Tetracentron* and *Zizyphoides* leaves; however, at present we would prefer to limit the designation of *Tetracentron* to those leaves with the well-defined characters of this genus.

While still of uncertain phylogenetic placement, the Trochodendraceae are clearly a family with a long evolutionary history and with greater diversity and a much wider distribution in the past in comparison to the family's present endemic occurrences. It is now clear that the Eocene of northwestern

North America was a significant time and place in the diversification of this interesting group.

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