

TROCHODENDRON AND NORDENSKIOLDIA (TROCHODENDRACEAE) FROM THE MIDDLE EOCENE OF WASHINGTON STATE, U.S.A.

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Fossil remains of the family Trochodendraceae are found in the early middle Eocene (49–50 Ma) Republic flora of northeastern Washington, a flora that contains a highly diverse and extensive montane warm-temperate assemblage. In this study, we document the earliest known fossil record of *Trochodendron* Sieb. & Zucc. (Trochodendraceae) based on the distinctive leaves of *Trochodendron nastae* Pigg, Wehr, & Ickert-Bond sp. nov., and two infructescences, and an isolated fruit assigned to *Trochodendron* sp. The Republic *Trochodendron* fruits are smaller but otherwise closely resemble those of extant *Trochodendron aralioides* Sieb. & Zucc. and those of Neogene fossil fruits. *Trochodendron nastae* leaves have the features of extant and other fossil *Trochodendron* leaves, except for their palmate rather than pinnate primary venation. This feature is more typical of the trochodendralean sister genus *Tetracentron* Oliver. *Trochodendron nastae* leaves have venation that thus appears to be intermediate between these two genera, suggesting that the palmate condition may be basal within this group. The Republic flora also contains one of the first known Eocene occurrences of the trochodendralean infructescence *Nordenskioldia* Heer in western North America, along with leaves similar to *Zizyphoides* Seward & Conway, its apparently congeneric foliar genus. The presence of two distinctive trochodendralean plants, *Trochodendron* and the *Nordenskioldia/Zizyphoides* plant at Republic, demonstrates that the Trochodendraceae were a diverse group of plants during the middle Eocene in western North America. This finding further documents the greater diversity during the Tertiary and wider distribution of a group known today exclusively from Asian endemics.

Keywords: basal eudicot, Eocene, *Nordenskioldia*, *Tetracentron*, *Trochodendron*, Trochodendraceae.

Introduction

The Trochodendrales includes two extant genera, *Trochodendron* Sieb. & Zucc. and *Tetracentron* Oliver, that have been recognized as either both within the family Trochodendraceae or sometimes split into two families, Trochodendraceae and Tetracentraceae (Smith 1945; Endress 1986; Endress and Igersheim 1999; Magallón et al. 1999). A clear understanding of the phylogenetic relationships of these plants remains in flux, but the group is most recently positioned within the basal eudicot grade as a sister group to the rest of the basal eudicots on the basis of combined molecular phylogenies (Magallón et al. 1999). A number of recent studies have confirmed the position of the Trochodendraceae within the basal eudicots (e.g., Graham et al. 2000; Kuzoff and Gasser 2000; Mathews and Donoghue 2000; Soltis et al. 2000).

Trochodendron aralioides Sieb. & Zucc., is a large, evergreen shrub or small tree that bears elliptical to obovate, coriaceous evergreen leaves in pseudoverticels and lacks vessels in its wood (Smith 1945). This tree is native to Japan, Taiwan, South Korea, and the Ryukyu Islands (Smith 1945; Mabblerley 1987). The closely related *Tetracentron sinense* Oliver, a deciduous tree occurring in Nepal, southwestern and central China, and northern Burma, has long and short shoots bearing

palmately veined, stipulate leaves. Both genera bear apetalous flowers in cymose inflorescences that develop into loculicidal capsules that dehisce to release numerous small, winged seeds (Smith 1945; Doweld 1998; Endress and Igersheim 1999). Like *Trochodendron*, *Tetracentron* also lacks vessels in its wood (Smith 1945).

While today's occurrence of these two genera is greatly restricted in both diversity and distribution, the family was widespread in the Northern Hemisphere during most of the Tertiary (Crane 1989; Crane et al. 1990, 1991; Manchester et al. 1991; Fields 1996a, 1996b; Manchester 1999). Trochodendroid fossil leaves ("trochodendrophylls") first appear during the Early Cretaceous (late Albian) in the Potomac Group of eastern North American coastal areas and persist into the Paleocene, with similar foliage types known in the mid-Cretaceous of other areas of North America and Eurasia (Crabtree 1987; Upchurch and Wolfe 1987; Crane 1989; Crane et al. 1991). These leaves, which are typified by actinodromous venation and often possess glandular, "chloranthoid" teeth (Hickey and Wolfe 1975), have been taxonomically difficult to interpret and have been allied with several different families. Reproductive remains of the extinct genus *Nordenskioldia* Heer are known from the Late Cretaceous of Alberta, Canada (Serbet 1997) and Asia (Vakrameev 1958; Manchester 1999). The Late Cretaceous wood assigned to the family, *Tetracentronites panochetris* Page, is described from the latest Campanian Panoche Formation of central California (Page 1968). The Early

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Cenomanian (Late Cretaceous) angiosperm flower, *Spanomera mauldinensis* Drinnan, Crane, Friis & Pedersen (Buxaceae) from the Potomac Group, also shares many features of the Trochodendrales (Drinnan et al. 1991; Manchester et al. 1991).

During the Paleocene, infructescences and isolated fruits of *Nordenskioldia borealis* (Heer) Crane, Manchester, & Dilcher and the associated leaves of *Zizyphoides flabella* (Newberry) Crane, Manchester, & Dilcher were widespread throughout the Northern Hemisphere, with occurrences in numerous localities of western North America, the Arctic, and Asia (Crane et al. 1990, 1991 and references cited therein; Manchester 1999). Leaves and reproductive remains of these genera persisted into the Eocene in eastern Asia (Crane et al. 1991) and also have been reported from the Canadian Arctic (McIver and Basinger 1999). They are represented in the Miocene of western North America in Idaho, Oregon, and Washington by *Nordenskioldia interglacialis* (Hollick) Manchester, Crane, & Dilcher and *Zizyphoides auriculata* (Heer) Manchester, Crane, & Dilcher (Manchester et al. 1991).

Leaves and reproductive remains of the genus *Trochodendron* are presently known from Miocene localities in western North America, Japan, and Kamchatka (Chelebaeva and Chigayeva 1988; Uemura 1988; Manchester et al. 1991; Fields 1996a, 1996b; Manchester 1999). While most Neogene fruit occurrences have been listed as *Trochodendron* sp., fruits from Kamchatka have been described as *Trochodendron kamtschaticum* Chelebaeva & Chigayeva and leaves as *Trochodendron evenense* Chelebaeva & Chigayeva (Chelebaeva and Chigayeva 1988). *Trochodendron* leaves from Japan found in association with infructescences are referred to the species *Trochodendron protoaralioides* Murai (Uemura 1988). The early Eocene London Clay taxon *Trochodendron? pausiseminum* Reid & Chandler (Reid and Chandler 1933), based on a single fragmentary specimen, was excluded from the family by Collinson (1983). Leaves described from the Paleogene of Alaska as *Tetracentron piperoides* Wolfe (Wolfe 1977) have not yet been found in association with fruits. Because of the lack of reproductive structures and the intergradation of this type of Alaskan leaf with other, particularly cercidiphyllaceous forms, their assignment to the Trochodendrales remains uncertain (S. R. Manchester, written communication, 2000).

Fossil trochodendralean wood has been recognized from a variety of Tertiary localities, including *Trochodendroxylon beckii* Hergert & Phinney that was first described from the Oligocene of Oregon (Hergert and Phinney 1954). Similar wood from the Eocene Clarno Formation of Oregon was found to be indistinguishable from extant *Trochodendron* by Scott and Wheeler (1982), who reassigned it to *T. beckii* (Hergert & Phinney) Scott & Wheeler. *Trochodendron* wood has also been recognized in Washington State (E. R. Strauss, written communication, 1996) from an Eocene occurrence at Alder Lake, near Etonville. A middle Tertiary wood from Greenland (Mathiesen 1932) has also been suggested to have trochodendralean affinities (Bailey and Nast 1945). To our knowledge, fossil pollen has not been reported for this family.

The family Trochodendraceae is well represented in the highly diverse, early middle Eocene (49–50 Ma) Republic flora of northeastern Washington State (Wolfe and Wehr 1987; Johnson 1996; Wing and DiMichele 1996). Infructescences,

fruits, and leaves have previously been attributed to aff. *Trochodendron* (Wolfe 1989; Wehr and Manchester 1996), while a *Nordenskioldia* infructescence and leaves of *Zizyphoides* have also been documented (Wehr 1995; Wehr and Manchester 1996). In this study, we describe these forms and name the new species *Trochodendron nastae* Pigg, Wehr, & Ickert-Bond sp. nov. for a distinctive leaf type that combines most of the features of previously known fossil and extant *Trochodendron* leaves but has the palmate primary venation typical of extant *Tetracentron*. Two compressed infructescences and an isolated fruit assignable to *Trochodendron* sp. also occur within the same flora. The Republic fossils represent the oldest record of *Trochodendron*, the genus having previously been known from Miocene strata of western North America, Japan, and Kamchatka (Manchester 1999). The *Nordenskioldia* sp. infructescence and *Zizyphoides* leaves also occurring at Republic provide some of the first evidence of Eocene representatives of these two genera for western North America (McIver and Basinger 1999). The presence at the Republic locality of two distinctive trochodendralean plants, *Trochodendron* and the *Nordenskioldia/Zizyphoides* plant, demonstrates that the Trochodendraceae were a diverse group in western North America during the middle Eocene. This evidence further documents their greater diversity and occurrence during the Tertiary in comparison to their current endemic Asian distribution.

Material and Methods

Specimens from the Republic, Ferry County Washington, flora are preserved as compression/impression fossils in lakebed sediments that are concentrated in mudstone- and sandstone-dominated deposits of the lower member of the early middle Eocene Klondike Mountain Formation. The Klondike Mountain Formation is one of the regional, unconformity-bounded units within the larger Challis sequence. The regional geology of the Republic area is dominated by grabens and other fault-bounded basins. The fossil-bearing formations are not deposited within local basins or grabens. Instead, the formations were preserved as a regional synform among metamorphic complexes (Cheney and Rasmussen 1996). Coeval fossil-bearing strata containing similar remains occur at Princeton (Allenby Formation), Quilchena and McAbee (Tranquille Beds, Kamloops Group), Driftwood Creek (Smithers), and other localities in the interior of British Columbia, Canada.

During the Eocene, from ca. 57 to 37 Ma, northern interior Washington State and interior British Columbia were the scene of intense volcanic activity (Gaylord et al. 1996). The extent and thickness of volcanic deposits indicate that the region known today as the Okanogan Highlands may have been a mountainous area during much of that epoch (Wing 1987). The ^{40}Ar - ^{39}Ar dating of volcanic rocks closely associated with the Republic flora and fauna limit the deposition of the Klondike Mountain Formation to between 50 and 49 Ma (B. Berger, written communication, 1992).

Specimens were photographed using Ektachrome 160 tungsten slide film with either a 35-mm camera on a copy stand or under an Olympus BHZ dissecting microscope. Some specimens were photographed under the Olympus dissecting scope using a polarizing ring illuminator to reduce surface glare and

enhance details of higher-order venation. Extant leaves studied for comparative purposes were cleared in a mixture of 50% hydrogen peroxide and 50% glacial acetic acid to reveal details of venation. Extant fruits were embedded using standard techniques and serially sectioned for study. Images were scanned with a Nikon LS-2000 Slide Scanner, burned onto CDs with an Adaptec Easy CD Creator 4 CD burner, and processed using Adobe Photoshop 5.0 software.

Fossil specimens are deposited at the Burke Museum of Natural History and Culture (UWBM) and at Stonerose Interpretive Center (SR) (Barksdale 2000), courtesy of Lisa Barksdale, who graciously provided material for study. Extant materials are housed in the Vascular Plant Herbarium and the Fossil Plant Collections at Arizona State University (ASU; table 1).

Systematics

Family—Trochodendraceae

Genus—Trochodendron Sieb. & Zucc. (1838)

Type Species—Trochodendron aralioides

Species—Trochodendron nastae Pigg, Wehr, et Ickert-Bond, sp. nov. (Fig. 1; Fig. 2A, 2B, 2D–2F; Fig. 3A, 3B, 3D–3H)

Specific diagnosis. Leaves simple, symmetrical, elliptical to obovate; 3.0–7.7 cm long (\bar{x} = 5.3 cm) \times 1.5–4.0 cm wide (\bar{x} = 2.9 cm); length-to-width ratio 1.4–3.6 : 1 (\bar{x} = 2.5 : 1); apex acuminate, base cuneate; petioles exstipulate and striate, up to 2.8 cm long \times 0.7–2.1 mm wide; leaves basally actinodromous, primary venation composed of a midvein and two pairs of lateral primaries, marginal vein present, secondaries produced from midvein alternately at acute angles. Secondary veins alternately produced from lateral primaries, lateral primaries dichotomizing distally, with veins entering marginal

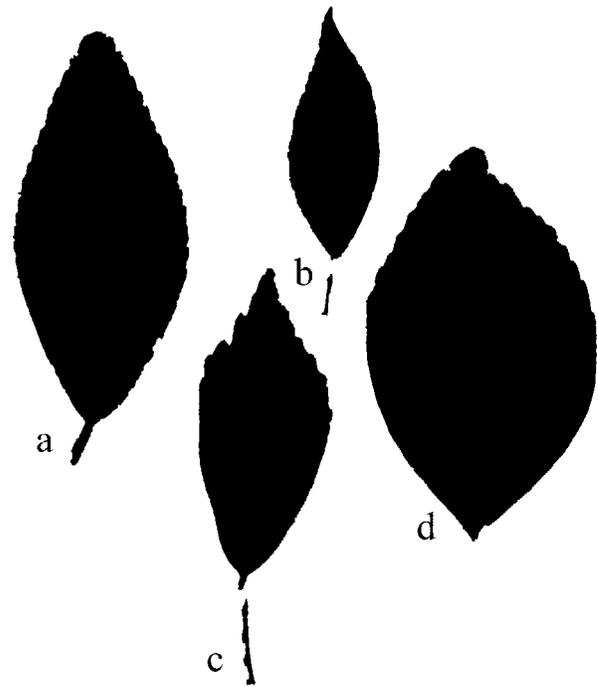


Fig. 1 Representative leaves of *Trochodendron nastae* sp. nov. Pigg, Wehr, & Ickert-Bond drawn to scale to show variation in size and shape. Leaf apex is incomplete in *a* and *d*. *a*, SR 98-2-1a. *b*, UWBM 54868. *c*, UWBM 96609a. *d*, UWBM 96612. All figures $\times 0.75$.

teeth in apical part of leaf. Secondary veins festooned brochidodromous, admedial secondary veins diverge from lateral primaries at angles of 40°–45°, joining weak intersecondary veins to form chevron-like braces; tertiary and quaternary order veins form four- to five-sided aeroles, fifth-order veins present; leaf margin unlobed crenate; distal three-fourths of margin toothed, basal one-fourth entire; teeth glandular, teeth straight apical, convex basal, leaf texture coriaceous.

Derivation of specific epithet. The specific epithet, *nastae*, is proposed in honor of Charlotte G. Nast, in recognition of her important contributions to the study of fossil and extant Trochodendrales (Bailey and Nast 1945).

Holotype. SR 98-2-1a (figs. 1A, 2A).

Paratypes. UWBM 31248a,b (fig. 3G), 31249 (fig. 3A, 3D, 3E), 31250a,b (fig. 2B), 54868 (figs. 1B, 2F), 96609a,b (fig. 1C), 96612 (figs. 1D, 2E), SR 88-2-2 (fig. 3B), 95-19-3a (fig. 3F, 3H), 95-23-15 (fig. 2D), UWBM 31251, 31252, 31257a,b, 36365b, 36834, 36964, 39731, 39754, 54714, 54808a,b, 56501, 56502, 56634, 56800, 56826a,b, 56827, 56828, 57444, 57445, 57448a,b, 57449, 57450, 57451a,b, 57452, 57453, 57454a,b, 71353, 74313 (=SR 92-3-12), 76494a,b, 76495a,b, 76496, 76498, 76499a,b, 76503, 76504, 76505, 96245, 96610, 96611, SR 89-12-4, 91-1-4, 91-8-4, 91-8-11, 93-1-1, 93-8-14, 95-9-2, 95-23-30a,b, 95-24-11, 95-25-35a,b, 96-9-36, 96-13-13, 97-6-4, 97-10-1a,b, 98-2-2, 98-3-1a,b, 98-3-2a,b, 98-3-3a,b.

Type locality. Republic, Ferry County, Washington.

Age and stratigraphy. Middle Eocene Klondike Mountain

Table 1

Extant *Trochodendron* Leaf Specimens Examined

Number	Locality	Habitat
ASU 108788	Japan, Nara Prefecture, Yoshino-gun, Tenkawa-mura, Mount Omine, Mount Dainichi	Ca. 1200 m elevation
ASU 168724	Taiwan; Taipei Hsien: Yangming Shan National Park north of Taipei City	Mixed, broad-leaved evergreen and deciduous forests; 430 m elevation
ASU 204150	Taiwan; northeastern district, Ilan State	Montane vegetation, mixed coniferous forests, subcanopy species; 1500 m elevation
ASU 235580-235582	Washington State, King County, Washington Arboretum, Seattle	Cultivated

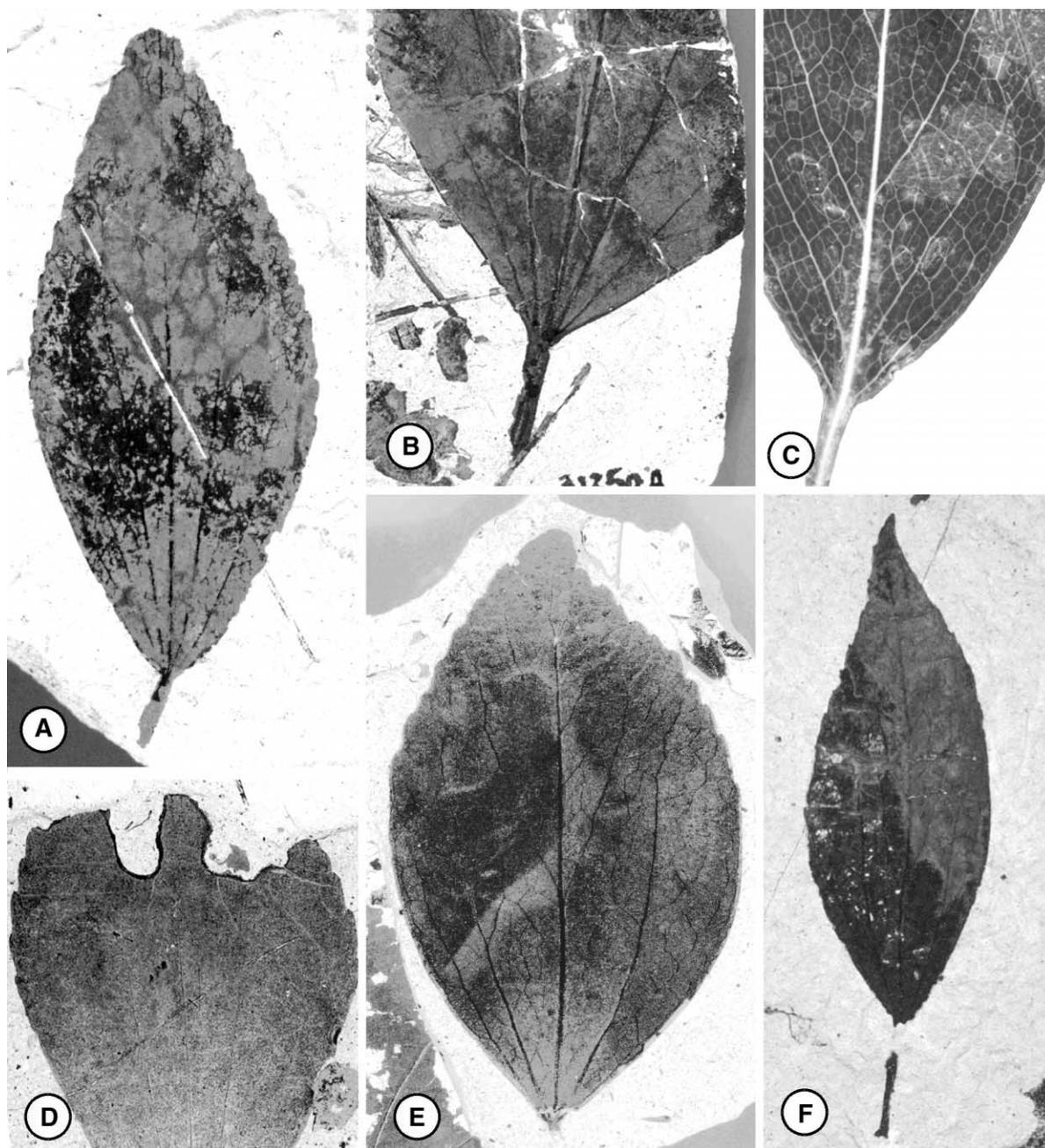


Fig. 2 *Trochodendron nastae* sp. nov. Pigg, Wehr, & Ickert-Bond (A, B, D–F), and *Trochodendron aralioides* (C) leaves. A, Holotype specimen showing basal palmate venation and crenate leaf margin. Apex is not complete. Note pine needle impressed diagonally on leaf surface. SR 98-2-1a, $\times 1.5$. B, Leaf base and petiole. Note palmate venation. Pine needle appressed to petiole was previously interpreted as stipule. UWBM 31250a, $\times 1.6$. C, Extant *T. aralioides* leaf, cleared to show details of venation. Note pinnate primary venation. The midvein is much thicker than the lateral veins, and secondary veins are farther apart toward top of the photograph. Cleared leaf, 1. ASU, $\times 1.6$. D, Leaf showing predation pattern and reaction zone (at top). SR 95-23-15, $\times 1.3$. E, Broad leaf showing several orders of venation. UWBM 96612, $\times 1.6$. F, Narrow leaf showing complete acuminate apex. UWBM 54868, $\times 1.2$.

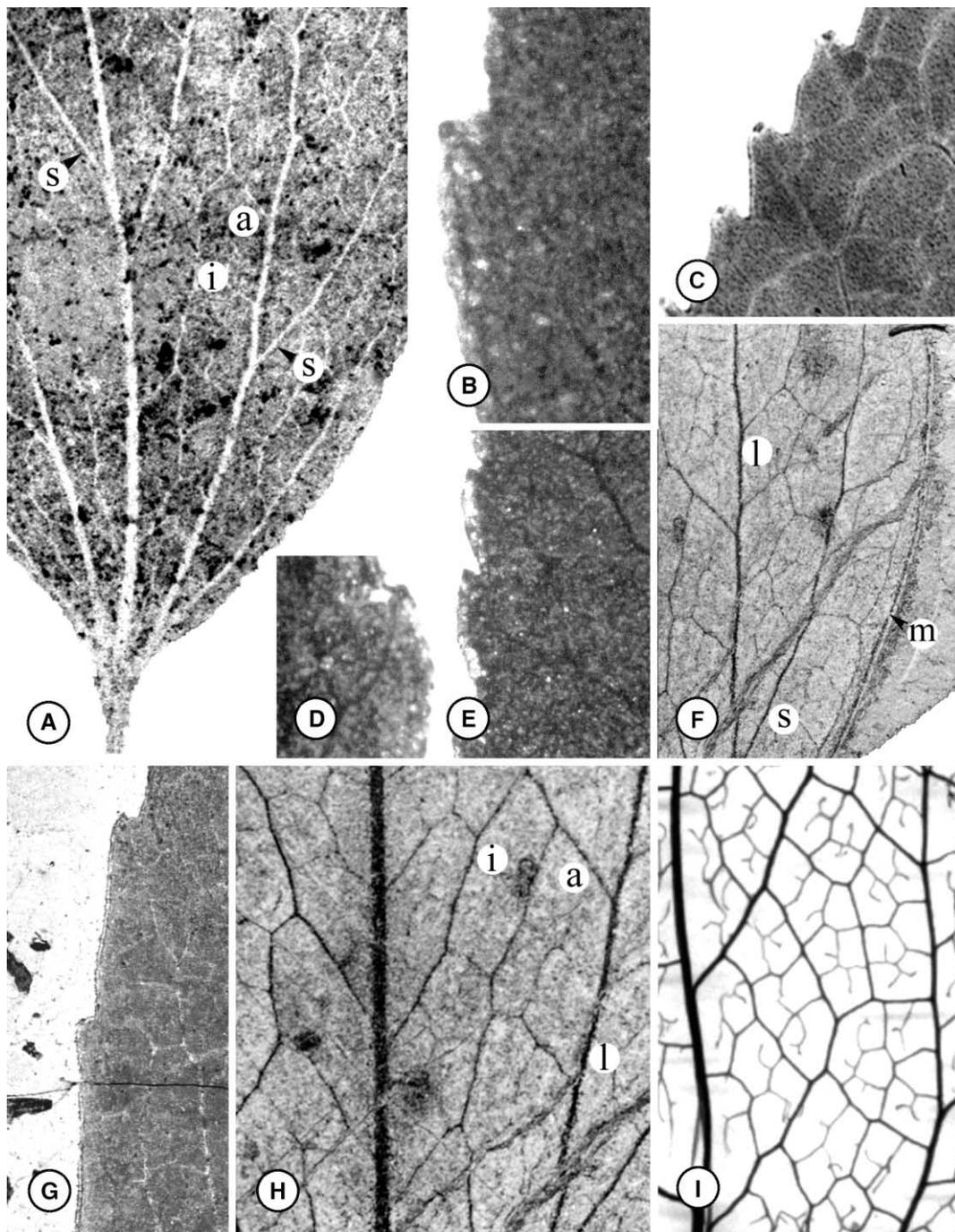


Fig. 3 *Trochodendron nastae* sp. nov. Pigg, Wehr, & Ickert-Bond (A, B, D-H); *Tetracentron sinense* (C) and *Trochodendron aralioides* (I) leaves showing details of leaf venation and margin. A, Leaf showing details of venation. Note midvein; two pairs of lateral primaries originating at base; secondary veins (s) produced by midvein and lateral primaries, weak intersecondaries (i), and admedial tertiaries (a). UWBM 31249, $\times 6.2$. B, Leaf margin showing detail of glandular tooth. SR 88-2-2, $\times 16$. C, Extant leaf of *Tetracentron*, to show detail of leaf margin and vascularized, glandular teeth, $\times 10$. D, Leaf margin showing venation of glandular tooth. UWBM 31249, $\times 8$. E, Leaf margin. UWBM 31249, $\times 8$. F, Lateral side of leaf showing lateral primary vein (l), secondary vein (s), marginal vein (m), and festooned brochidodromy. SR 95-19-3a, $\times 1.2$. G, Leaf margin showing marginal vein and distantly spaced teeth. UWBM 31248a, $\times 3$. H, Leaf showing midvein, lateral primary (l), weak intersecondary (i) joining admedial tertiary (a) (at top), and aereoles. Higher-order veins are faintly visible. SR 95-19-3a, $\times 1.9$. I, Extant *Trochodendron* leaf, cleared to show venation details. Compare with H. Cleared leaf, ASU, $\times 7$.

Formation, 50–49 Ma (B. Berger, written communication, 1992).

Results

Trochodendron nastae sp. nov. Leaves

This description is based on a total of 66 leaves (11 nearly complete and 55 fragmentary specimens), many of which are well preserved and show good detail of venation and leaf margin (fig. 1; fig. 2A, 2B, 2D–2F; fig. 3A, 3B, 3D–3H). The leaves are simple and symmetrical. The lamina is elliptical to more rarely obovate (fig. 1; fig. 2A, 2E, 2F) and is 3.0–7.7 cm long, with an average length of 5.3 cm (based on 24 leaves with complete lengths), and 1.5–4.0 cm wide, with an average width of 2.9 cm (based on 44 leaves with complete widths). The length-to-width ratio is 1.4–3.6 : 1 with an average of 2.5 : 1 (based on 11 leaves with both complete lengths and widths). These fossil leaves show a similar range of variability in shape when compared to extant *Trochodendron aralioides* and fall along the smaller side of size range in leaves we examined from herbarium sheets (table 1). Like extant *T. aralioides*, the apex of the lamina, when present, is acuminate (fig. 2F), and the leaf base is cuneate (fig. 1; fig. 2A, 2B, 2F). Petioles are up to 2.8 cm long and 0.7–2.1 mm wide. They are exstipulate and striate (fig. 2A, 2B, 2F). Some leaves have petioles that are slightly enlarged (up to 3 mm) at the base, possibly resulting from insect damage (C. Labandeira, written communication, 1998). Additionally, some leaves show “external foliage feeding in the form of excellent margin feeding with well-developed reaction rims” (fig. 2D; C. Labandeira, written communication, 1998).

The primary venation of *Trochodendron nastae* is basally actinodromous, or palmate, with a central midvein and two pairs of lateral primaries (fig. 2A, 2B, 2E; fig. 3A). The width of the midvein is fairly uniform, thinning slightly in the apical portion of the lamina, and it is straight through most of its length, sometimes becoming sinuous distally and almost extending to the acuminate apex of the leaf. In contrast, leaves of extant *T. aralioides* have pinnate primary venation with a prominent midvein that is several times thicker than the laterals (fig. 2C). The innermost lateral primary veins of *T. nastae* extend most of the length of the leaf, fork apically, and enter marginal teeth in the apical portion of the leaf (figs. 2A, 3A). The outer lateral primary veins arc out near the leaf margin about one-third of the distance from the base (figs. 2E, 3A). Angles between adjacent lateral primaries are fairly acute as are those between the lateral primaries and the midvein. Secondary veins are produced alternately from the midvein in the upper half of the lamina, distal to the area of divergence of the lateral primaries (figs. 2E, 3A). Secondary veins are also produced alternately from lateral primaries (fig. 2A). Weak intersecondary veins are present between lateral primaries and parallel them in basal areas of the leaf. In more apical areas of the leaf, they occur between and run parallel to the secondary veins produced by the midvein. These weak intersecondaries meet the admedial veins that diverge from the lateral primaries at 40°–45°. These two veins meet to form occasional chevrons or bracings across the central part of the lamina (fig. 3A, 3F, 3H), similar to those of *T. aralioides* (fig.

3I). Tertiary veins paralleling the weak intersecondaries and quaternary veins form aeroles that are four-to-five sided, another feature similar to that of extant *T. aralioides* (fig. 3F–3I). Fifth-order veins can occasionally be recognized, but their features are obscure (fig. 3H). Toward the leaf margin, secondaries form a double set of loops, resulting in festooned brochidodromy (fig. 3F). A marginal vein runs along the leaf margin (fig. 3F, 3G).

The leaf margin is unlobed crenate with numerous small, appressed glandular teeth in the apical three-fourths of the lamina (fig. 2A, 2E; fig. 3B, 3D, 3E, 3G). This type of margin is similar to those in apical portions of modern examples of *Trochodendron* and *Tetracentron* (fig. 3C). The lower one-fourth portion of the lamina is entire (fig. 2A, 2E, 2F; fig. 3A). Teeth are glandular, straight apical, convex basal (Leaf Architecture Working Group 1999). The leaf texture is coriaceous. Cuticle is not well preserved.

Associated Trochodendron Infructescences and Fruits

Two *Trochodendron* infructescences, one a part-counterpart specimen, both bearing attached fruits and one isolated fruit, are known (fig. 4A–4C, 4E–4I). The most complete infructescence (fig. 4A, 4B) consists of a striated woody axis, 5.4 cm long and 0.8–1.0 mm in diameter (fig. 4G), bearing fruits on striated peduncles that average 5 mm in length. Up to 10 attached fruits and the peduncles of two more can be seen (fig. 4A, 4B). Fruits are 1.85–2.5 mm long and 2.0–3.7 mm wide and have an acute base and broadened apex (fig. 4C, 4E, 4F, 4I). Depending on the angle of compression of specimens, fruits vary in shape from an inverted triangle to more elongate and obovate (fig. 4C, 4E, 4F, 4I). Many fruits (fig. 4E, 4I) bear the remnants of five to nine persistent styles like those seen in extant *T. aralioides* (fig. 4D). Major veins can be recognized on counterpart surfaces of fruits (fig. 4F, 4I), suggesting that vasculature was similar in fossils as it is in the living fruits (fig. 4D). An isolated fruit found in the matrix is 3.8 mm high × 5 mm wide (fig. 4H) and has a similar shape to those found in attachment and to those of extant *T. aralioides* (fig. 4D). Stamen and staminode scars could not be identified on fruits, and, unlike some Neogene fossils, nectaries were not obvious on the fruit bodies, probably because of limited preservation.

Nordenskioldia sp. *Infructescence and Zizyphoides-like Leaves*

One infructescence of *Nordenskioldia* has been found at Republic. The specimen consists of a woody axis 5.7 cm long × 2.3 mm wide with two helically borne sessile, attached fruits and the umbrella-shaped scar traces of three additional fruits (fig. 5A, 5B). Fruits are 6 mm high × 8 mm across. The best-preserved fruit consists of ca. 18 wedges and is obliquely oriented (fig. 5B).

Numerous leaves that are very similar to Paleocene *Zizyphoides flabella* and Miocene *Zizyphoides auriculata* are also found at Republic (fig. 5C). They are simple and symmetrical with long petioles, actinodromous primary venation, festooned brochidodromy, and an apically toothed margin. Leaves of this type, sometimes attributed to *Zizyphoides*, are highly variable and intergrade morphologically with those of several other

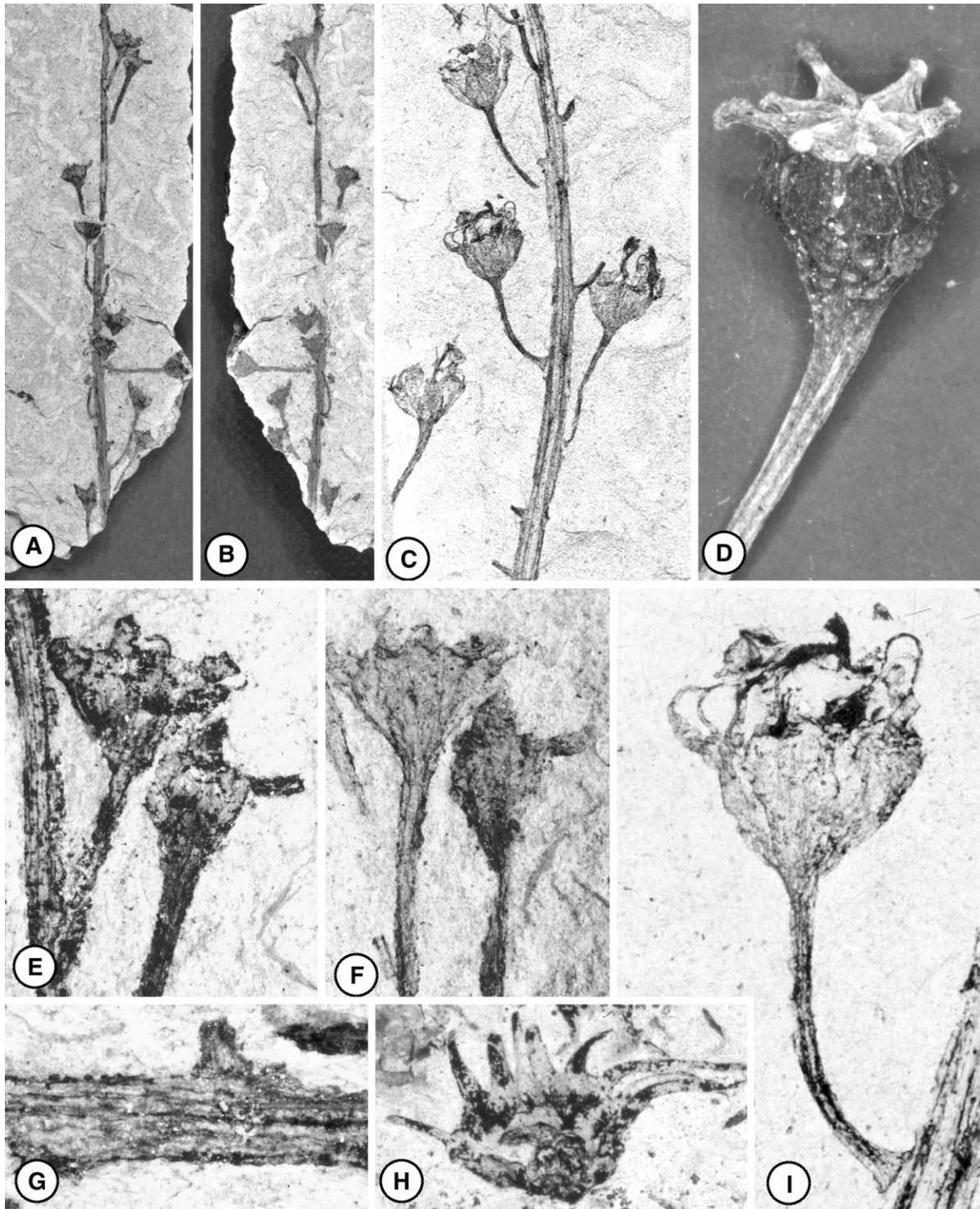


Fig. 4 Fossil *Trochodendron* sp. infructescences and fruits (A–C, E–I) and extant *Trochodendron aralioides* fruit (D). A, Cymose infructescence bearing fruits. Counterpart of B. UWBM 94570a, $\times 1.6$. B, Cymose infructescence bearing fruits. Counterpart of A. UWBM 94570b, $\times 1.6$. C, Infructescence with three attached fruits. SR 00-01-02, $\times 4.1$. D, Extant *Trochodendron* fruit. Note striate peduncle, stamen scars, nectariferous areas, and persistent styles, $\times 7$. E, Detail of A to show fruit shape and persistent styles. Counterpart of UWBM 94570a, $\times 9$. F, Detail of B. Figure has been inverted horizontally to maintain orientation with E. Note venation on fruit body. UWBM 94570b, $\times 9$. G, Detail of infructescence axis showing striations and base of a peduncle. UWBM 94570a, $\times 11$. H, Individual fruit with eight persistent styles. UWBM 74492a, $\times 11$. I, Detail of C to show attached fruit with long peduncle, venation of fruit, and remnants of styles. SR 00-01-02, $\times 14$.

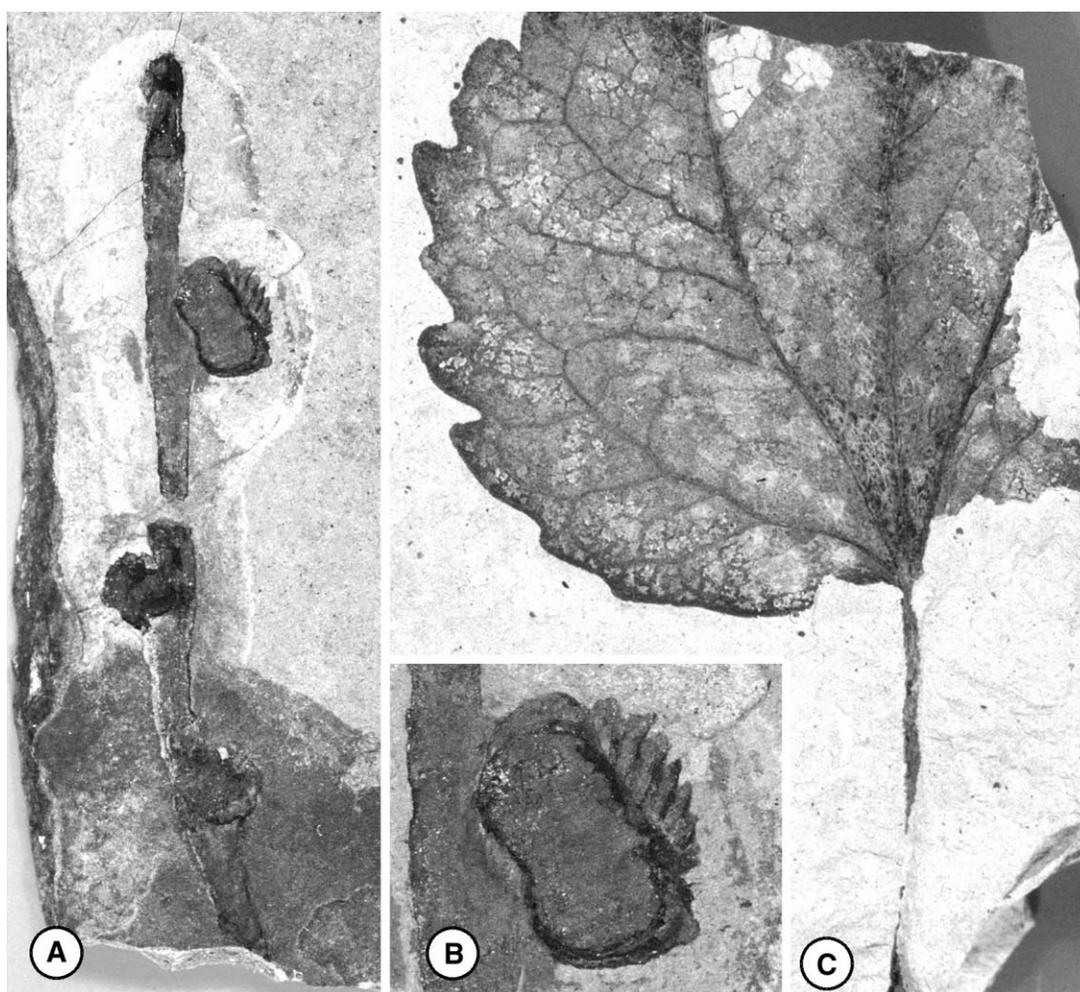


Fig. 5 *Nordenskioldia* sp. infructescence and fruit (A, B) and *Zizyphoides* sp. leaf (C). A, *Nordenskioldia* sp. infructescence showing one attached fruit and two additional attachment scars. UWBM 74314, $\times 2.1$. B, Detail of *Nordenskioldia* sp. fruit. UWBM 74314, $\times 4$. C, *Zizyphoides* sp. leaf showing long petiole, actinodromous venation, and festooned brochidodromy, UWBM 76490b, $\times 2.5$.

taxa, particularly cercidiphyllaceous forms. They were not investigated in detail in this study.

Discussion

Trochodendron nastae Leaves

The leaves described herein as *Trochodendron nastae* represent the oldest currently known leaves that can be confidently assigned to the genus *Trochodendron*. *Trochodendron nastae* is assignable to *Trochodendron* on the basis of a combination of morphological features, including elliptical/obovate shape, acuminate apex, cuneate base, coriaceous texture, and lack of stipules (table 2). Only the presence of palmate rather than pinnate primary venation separates this leaf type from extant *Trochodendron* and other related Neogene fossil leaves. Because of this distinctive feature, we propose the new species *T. nastae*. *Tetracentron*, the most closely related genus to *Trochodendron*, shares many features but is notably distinct in a number of other characters (table 2). Additional features

of venation, such as festooned brochidodromy, admedial secondary veins and weak intersecondaries forming chevron bracing, marginal veins, and glandular teeth characterize *Trochodendron* and several other genera (e.g., Crane et al. 1990).

Representatives of the leaves documented in this study were first described by Wolfe (1989) as “the Republic taxon.” In his study, several features were noted that distinguished leaves of this type as of trochodendrolean affinity, including “intercostal venation composed of an intersecondary vein that is joined by widely and irregularly spaced, orthogonal tertiary veins; festooned brochidodromy; well-developed, admedially ramified bracing of the axils of the secondary veins; chevron-like braces between the major basal veins; and numerous chloranthoid teeth” (Wolfe 1989, p. 77). Since this initial study, we have obtained a much larger sample size of these leaves, enabling us to characterize more completely the morphological variation present in *T. nastae* (fig. 1; fig. 2A, 2B, 2E, 2F). Based on the larger sample, it is apparent that leaves of *T. nastae* are most typically elliptical in shape or, more rarely, obovate. Some leaves illustrated by Wolfe (1989, fig. 5-1B, 5-1C) and de-

scribed as almost rhomboidal are misleading because they have incomplete laminae. On the basis of one specimen Wolfe (1989) considered leaves assignable to *T. nastae* to be stipulate (fig. 5-1D of Wolfe 1989). Our reexamination of this specimen suggests that the structure identified as a stipule is a pine needle impressed over the petiole and appears to be on a different bedding plane than that of the *T. nastae* leaf (fig. 2B). Pine needles are relatively common in association within the leaf-bearing matrix (fig. 2A, 2B).

As the oldest currently known *Trochodendron* leaves, *T. nastae* leaves show a combination of mostly typical *Trochodendron* features coupled with actinodromous venation, a feature found in the closely related genus *Tetracentron* and thought by some to be the more basal venation form in this group of plants (Wolfe 1989; Manchester 1999). In comparing venation of *T. nastae* with that of extant *Trochodendron aralioides* (figs. 2C, 3A), the transition between the two venation types may not be all that drastic. Slight changes in the relative distance between lateral veins in the basal portion of the leaf could result in the transition between the “crowded” palmate venation of *T. nastae* and the pinnate condition of *T. aralioides*. This, with an increase in overall size of the midrib, could result in the venation pattern of extant *Trochodendron*. In contrast to the broad, often cordate base of *Tetracentron*, which, essentially, has “room” for palmate venation, *Trochodendron* leaves are characterized by a much narrower cuneate base (fig. 2A–2C). If the palmate condition is indeed basal within the group, as some have suggested (e.g., Wolfe 1989), then this correlation of leaf base shape and change in venation could easily follow.

Trochodendron Reproductive Remains

The *Trochodendron* sp. infructescences and isolated fruit from Republic are very similar to both those of the extant *T. aralioides* (fig. 4D) and previously described Neogene specimens from the middle Miocene of western North America (Manchester et al. 1991; Fields 1996a, 1996b), Kamchatka (Chelebaeva and Chigayeva 1988), and the late Miocene of Japan (Uemura 1988). All fossil remains of *Trochodendron* infructescences are morphologically very similar to those of extant *T. aralioides* (Manchester et al. 1991). The Miocene forms show similarities to extant *Trochodendron* in fruit shape, presence of striate peduncles and infructescence axes, persistent stigmas, and, in some cases, nectaries on the basal portions of fruits (Manchester et al. 1991). While many of

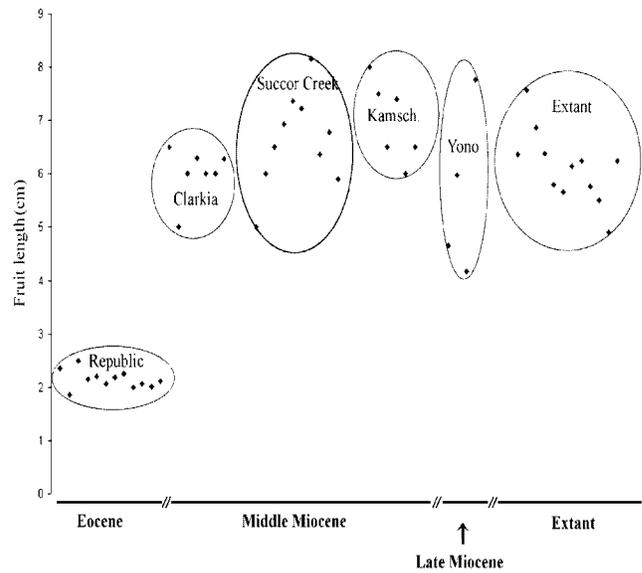


Fig. 6 Scatter diagram showing fruit-length variation of *Trochodendron* in relation to age and occurrence. Each known fruit specimen per locality is plotted within the circle labeled by that locality, and data points are separated for clarity. Localities are placed on the X-axis in general stratigraphic order. Stratigraphic positions are not to scale and not continuous. Three overlapping middle Miocene floras (Clarkia, Succor Creek, and Kamchatka) are separated for clarity. Republic (this study), Clarkia (Manchester et al. 1991; Fields 1996a), Succor Creek (Fields 1996a), Kamchatka (Chelebaeva and Chigayeva 1988; S. R. Manchester, written communication, 2000), Yonosawa (Uemura 1988), and extant (Crane 1989; Manchester et al. 1991; this study). Abbreviations: *Kamsch* = Kamchatka, *Yono* = Yonosawa.

these same features are seen in the Republic specimens, the apparent lack of nectaries is probably preservational. When fruit size of fossil and representative extant specimens is plotted, however, the Eocene Republic fruits are considerably smaller in size than both Miocene and extant forms (fig. 6). Because we find no distinctive features besides this size difference in the Republic form, we feel that there is little reason to establish a new species for these infructescences and fruits, which are found in association and not organic connection to *T. nastae* leaves, and thus prefer to call them *Trochodendron* sp. This taxonomic decision concurs with that of Manchester

Table 2

Comparison of Leaf Character Differences among *Trochodendron* Species and *Tetracentron*

	<i>Tetracentron</i>	<i>Trochodendron nastae</i>	<i>Trochodendron aralioides</i>
Shape	Ovate	Elliptical/obovate	Elliptical/obovate
Texture	Chartraceous	Coriaceous	Coriaceous
Stipules	Present	Absent	Absent
Primary venation	Palmate	Palmate	Pinnate
Pedicels	Short	Long	Long
Leaf apex	Acute	Acuminate	Attenuate
Leaf base	Cordate	Cuneate	Cuneate
Serration	Entire leaf	Distal three-fourths of leaf	Distal three-fourths of leaf

Sources. Data from Bailey and Nast 1945, Smith 1945, and this study.

et al. (1991) who suggested there was no reason to distinguish Neogene fruits from the extant forms.

Nordenskioldia and *Zizyphoides*

The Republic specimen of *Nordenskioldia* is among the first recorded in the Eocene of North America (McIver and Basinger 1999). The earliest fruits assigned to *Nordenskioldia* have been documented from the late Cretaceous of Asia and western Canada (table 3; Vakrameev 1958; Serbet 1997; Manchester 1999). While the Asian material is very similar to other younger *Nordenskioldia* species (S. R. Manchester, written communication, 2000), the Canadian fossils from Drumheller, Alberta, have a more unusual appearance (Serbet 1997). They are characterized by infructescence axes with very short internodes bearing numerous helical fruit scars, each with up to 21 points of fruitlet attachment. Isolated fruitlets and small (1.3 mm long), winged seeds have also been found along with one isolated leaf of possible trochodendrolean affinity (Serbet 1997). *Nordenskioldia* is best documented from numerous Paleocene floras of western North America, the Arctic, and Asia and Miocene floras of western North America. The Paleocene *Nordenskioldia borealis* and Miocene *Nordenskioldia interglacialis* are comparable in basic structural organization and resemble one another greatly (Crane et al. 1991; Manchester et al. 1991). Infructescence, fruit and seed size, and morphology are all similar (table 3). The most notable differences are in number of fruitlets per fruit and apparent dispersal method. Whereas *N. borealis* bears 12–20 fruitlets per fruit, the younger fruitlets of *N. interglacialis* number 14–29 per fruit. As in the Cretaceous Alberta material, isolated fruitlets and small, winged seeds occur commonly in the matrix in the Paleocene species, whereas in the Miocene, complete fruits are more often found separated from the parent axis. Isolated Miocene fruitlets are very rare and separate seeds have not been recovered. These findings have suggested to some authors that while Paleocene *Nordenskioldia* fruits apparently broke up into fruitlets and seeds were dispersed, in the Miocene, it may have been the entire fruit that acted as the dispersal agent (Manchester et al. 1991). In comparison to these forms, Eocene material of *Nordenskioldia* has been documented from the High Arctic but not described in detail (McIver and Basinger

1999). The Republic fruits are of comparable size and morphology to other fossil remains and greatly resemble the Paleocene and Miocene forms (S. R. Manchester, personal communication, 2000). No isolated seeds or fruitlets have been recovered, and it is not known whether fruits, fruitlets, or seeds acted as dispersal agents.

Affinities of *Nordenskioldia* with the Trochodendraceae first suggested by Kryshstofovich (1958) have been further established recently (Crane 1989; Crane et al. 1990, 1991; Manchester et al. 1991). Anatomically preserved *Nordenskioldia* infructescences from the Paleocene Almont, North Dakota, locality showed that, like *Trochodendron* and *Tetracentron*, these plants lack vessels in their wood and have similar pitting patterns on tracheary elements (Crane et al. 1990, 1991). The other major feature that *Nordenskioldia* shares with *Trochodendron* is its characteristic fruit structure composed of numerous whorled carpels, each of which retains an admedially recurved, persistent style. A number of features in which *Nordenskioldia* differs from *Trochodendron* include its separation into fruitlets, reduction to only one viable seed per locule, both the lack of nectaries and of the characteristic “hairpin” loop in the raphe, and other differences in seed vasculature and seed coat surfaces (Crane et al. 1991).

In a recent study of *Trochodendron* and *Tetracentron* fruit and seed anatomy, Doweld (1998) has questioned their taxonomic affinities with *Nordenskioldia*. He notes that while *Trochodendron* and *Tetracentron* are loculicidal capsules that release their winged seeds, the infructescence of *Nordenskioldia* is a compound structure that breaks down during dehiscence to produce fruitlet disseminules and leaves behind an empty central stalk. He interprets this type of fruit organization as more similar to one that occurs in the Theales.

This alternative suggestion of *Nordenskioldia*'s phylogenetic relationship, based on the interpretation of fruit structure alone, is not supported by other means. Based on current information, we believe the taxonomic position of *Nordenskioldia* within the Trochodendraceae remains justified. While *Nordenskioldia* clearly differs from *Trochodendron* and *Tetracentron* in features noted above, this relationship is strongly supported by the similarities in fruit structure and lack of vessels in the wood of *Nordenskioldia*, *Trochodendron*, and *Te-*

Table 3

Comparison of *Nordenskioldia* Infructescences

Taxon	<i>Nordenskioldia</i> sp. (1)	<i>Nordenskioldia</i> sp. (2)	<i>Nordenskioldia borealis</i> (3)	<i>Nordenskioldia</i> sp. (4)	<i>Nordenskioldia interglacialis</i> (5)
Age	Santonian	Maastrichtian	Paleocene	Middle Eocene	Miocene
Infructescence (l × w, cm)	—	2.5 × 1.0	17 × 0.3	5.7 × 0.2	9.5 × 0.12–0.3
Fruit height (mm)	7	—	8–10	6	7–8
Fruit major width (mm)	8.5	—	12–15	8	9–12.5
Minor width (mm)	—	—	—	—	9–12
No. fruitlets/fruit	14–16	up to 21	12–20	18	(14)–18–24–(29)
Fruit scar diameter (mm)	—	6	10	—	—
Fruitlet height (mm)	—	6	6.5	—	—
Fruitlet major width (mm)	—	4.5	3.8	—	—
Fruitlet minor width (mm)	—	1	1	—	—
Seed (l × w, mm)	—	1.3 × 0.53	5–8 × 4.5–6	—	7 × 3.5

Sources. Data from 1, Vakrameev 1958, Manchester 1999, S. R. Manchester, written communication; 2, Serbet 1997; 3, Crane et al. 1990; 4, this study; and 5, Manchester et al. 1991.

tracentron. While Doweld's (1998) ideas are intriguing, there seems to be no particular reason to ally this fossil infructescence more closely with the Theales, as he suggests, all of which have wood that contains vessels. The Republic specimen of *Nordenskioldia* adds no new information to the question of phylogenetic relationships. Until additional, taxonomically useful features, such as pollen and floral structure, become known for *Nordenskioldia*, assignment to Trochodendraceae continues, in our opinion, to be warranted and well documented by a number of authors.

Trochodendrolean Phylogeography and Evolution

In looking at the currently known phylogeographic distribution of *Nordenskioldia* and *Trochodendron*, an interesting pattern emerges (Manchester 1999). *Nordenskioldia* first appears in both North America and Asia during the Cretaceous and remains circumboreal in distribution during the Paleocene, having its last known occurrence in the Miocene of western North America. *Trochodendron*, however, first appears in the Eocene of western North America, is present in North America and Asia in the Miocene, and remains as a restricted, endemic taxon in Asia today. Although *Nordenskioldia* is currently the stratigraphically older known taxon, there is no particular reason to think it is directly ancestral to *Trochodendron*, particularly in light of what appears to be its greater complexity in fruiting structures. Similarities in vegetative as well as reproductive structures also link these taxa, particularly the vesselless wood anatomy and features of leaf morphology. It is interesting that *Zizyphoides*, the presumed leaf of *Nordenskioldia*, shares actinodromous venation with *Trochodendron nastae*, further supporting this feature as more basal within the group.

It may be that *Trochodendron* and *Nordenskioldia* are only a small part of the diversity of a larger group of taxa.

Trochodendrophyllous leaves in the Cretaceous may represent earlier evidence of this group, but they have yet to be linked with reproductive structures. As Lower Cretaceous mesofloras continue to yield exceptionally preserved remains with increasing diversity, the potential discovery of older trochodendrolean fruits appears highly possible. Given the enigmatic but apparently basal position of Trochodendrales based on combined molecular data sets (e.g., Magallón et al. 1999), it is likely that this is an ancient group of angiosperms and that further discoveries of older fossil remains will help resolve the phylogenetic position of this intriguing group.

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