

NEWLY RECOGNIZED DIVERSITY IN TROCHODENDRACEAE FROM THE EOCENE OF WESTERN NORTH AMERICA

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The Eocene flora of the Okanogan Highlands in the Pacific Northwest of North America has been recognized previously to include extinct species of both extant genera of the Trochodendraceae. Here, using microcomputed tomography (μ CT) scanning to augment traditional methods, we recognize additional diversity, including two new fruit types. *Concavistylon wehrri* sp. nov. is documented by a fertile twig with attached leaves and an infructescence, allowing for an unusually complete reconstruction of this extinct genus. *Concavistylon wehrri* infructescences are racemes bearing fruits on short pedicels. Fruits are apically dehiscent capsules with four to six styles. The leaves resemble those of modern *Trochodendron* in pinnate venation, glandular teeth, and epidermal anatomy but have short petioles. The second new type of infructescence, *Pentacentron sternhartae* gen. et sp. nov., resembles extant *Tetracentron* in having small, sessile, apically dehiscent capsules but consistently has five, rather than four, styles. The μ CT X-ray imaging demonstrates that fruits of both *Concavistylon* and *Pentacentron* differ from those of extant Trochodendraceae in having styles that are concave with stigmas directed inward rather than outward. These fossils, together with previously recognized fossil fruits and leaves of *Trochodendron* and leaves of *Tetracentron* from the same beds, indicate that the Trochodendraceae family was more diverse 50–52 Ma than it is today.

Keywords: British Columbia, *Concavistylon*, fruits, infructescences, leaves, McAbee, Republic, Washington, Tertiary, *Tetracentron*, *Trochodendron*.

Introduction

Eocene shales from the Okanogan Highlands of the Pacific Northwest in North America document early diversity of the eudicot family Trochodendraceae. Both of the extant genera, *Trochodendron* Sieb. & Zucc. and *Tetracentron* Oliver, have been documented previously in Eocene shales of Washington and British Columbia (Pigg et al. 2001, 2007). This is interesting because these genera are now monotypic and endemic to east Asia. Paleobotanical evidence indicates that both of them were distributed in western North America through at least the Middle Miocene (e.g., Manchester et al. 2018). Reproductive axes found at the Republic, Washington, locality in association with leaves of *Trochodendron nastae* Pigg, Wehr & Ickert-Bond are quite similar to those of fossil Miocene and extant forms, except for their small size (Pigg et al. 2001). A more robust infructescence, *Trochodendron drachukii* Pigg, Dillhoff, DeVore, and Wehr was described from McAbee, British Columbia (Pigg et al. 2007). *Tetracentron hopkinsii* Pigg, Dillhoff, DeVore, and Wehr leaves are

known also from the Eocene One Mile Creek site in British Columbia. In addition to the extant genera, it has become clear that some extinct representatives of the family resided in western North America during the Tertiary. For example, *Concavistylon* Manchester, Pigg & DeVore was recognized recently on the basis of infructescences from the middle Miocene of Oregon (Manchester et al. 2018).

Here we recognize two more representatives of Trochodendraceae from the Okanogan Highlands Eocene flora: *Concavistylon wehrri* sp. nov. and *Pentacentron sternhartae* gen. nov. New microcomputed tomography (μ CT) from X-ray scan data, showing details hidden within the shale, has provided important characters for the identification of these new species. A fertile twig bearing both fruits and foliage provides a firm basis for describing vegetative as well as fertile morphology of *Concavistylon*. In addition, specimens with cuticle preserved allow for the description of epidermal characters previously undocumented for fossil leaves of Trochodendraceae.

In the present study, we describe these additions to the fossil record of Trochodendraceae and summarize all of the taxa now recognized from the Eocene Okanogan Highlands flora for comparison with fossil occurrences of this family known elsewhere in the Northern Hemisphere. These records indicate greater morphological diversity in this family during the Eocene than today.

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Material and Methods

We focused on fossils from two main sites within the early-middle Eocene Okanogan Highlands localities, ca. 50–52 Ma (DeVore and Pigg 2010; Greenwood et al. 2016): the Republic flora from the town of Republic (Ferry County), northeastern Washington (Wolfe and Wehr 1987; Wehr and Hopkins 1994), and the McAbee flora near Cache Creek, British Columbia (Dillhoff et al. 2005; Gushulak et al. 2016). Specimens are archived at the Burke Museum of Natural History and Culture, University of Washington, Seattle (UWBM); the Stonerose Interpretive Center, Republic, Washington (SR); Thompson Rivers University, Kamloops, British Columbia (TRU); and Florida Museum of Natural History, Gainesville, Florida (UF). The holotype specimen of *Concavistylon wehrü* did not initially show the physical connection of fruits and foliage (fig. 1C), but the connection was subsequently exposed by chipping away the overlying sediment with fine needles while observing it with a dissecting microscope (fig. 1B, 1D).

Cuticles from leaves in the shales of the Boot Hill locality at Republic (UWBM locality B4131) and McAbee (UWBM locality B5751) were recovered by mechanical removal from the rock surface, cleaned in hydrofluoric acid, and macerated slightly with 5% potassium hydroxide. Fragments were washed in distilled water and placed in glycerine, covered with a coverslip, and photographed with Nomarski interference contrast optics. In addition, cuticles were examined by epifluorescence with a Zeiss photomicroscope using an H546 green excitation filter set (15) with a wavelength of 546 nm.

Leaves and infructescences were photographed by reflected light with a Canon Rebel XSI digital single-lens reflex camera with an EF-S60-mm macro lens. Additional images were obtained from data sets compiled by μ CT. The scanning of impression specimens in shale was performed at the University of Florida College of Engineering Nanoscale Research Facility with a GE Phoenix V|tome|x240 CT scanner, using a Tungsten reflection target and 0.5-mm copper filter, with a voltage of 210 kV and current of 170 μ A with 2250 images with a voxel size of 41 μ m. Data sets reconstructed as tiff stacks from the μ CT scans were analyzed with Avizo 9.0 Lite (FEI Visualization Science Group, Bordeaux, France) and exported as Stanford PLY files for further examination and image production using Meshlab (<http://www.meshlab.net/>). More details about the methodology for our applications of Avizo and Meshlab are provided in Manchester and Balmaki (2018).

Systematic Paleobotany and Description

Family—*Trochodendraceae* Eichler

Genus—*Concavistylon* Manchester, Pigg & DeVore 2018

Type species. *Concavistylon kvacekii* Manchester, Pigg & DeVore from the Miocene of Oregon (Manchester et al. 2018).

Species. *Concavistylon wehrü* sp. nov. (figs. 1–5).

Species diagnosis. Infructescence a raceme; axillary on vegetative stem; inflorescence axis 3 mm thick at base, narrowing to less than 1 mm distally. Fruits capsular, 5–7 mm wide, 5–6 mm high; pedicels short, 0.5 mm thick, 3–5 mm long, curved

uniformly toward infructescence apex. Styles persistent, 4, 5, or 6 (variable); 1.9–2.9 mm long, arising subequatorially, curving toward the fruit apex; elliptical bulge (interpreted as nectary) beneath each style. Capsules smooth, with a basal thickening and whorl of perianth scars at junction with pedicel. Dehiscence apical, with separation initiating immediately above each style and joining apically to form a 4-, 5-, or 6-rayed starlike opening.

Twig bearing simple leaves in alternate phyllotaxy. Terminal bud 1 cm long, 5 mm wide, elongate, pointed apically; axillary bud 8 mm long, 1.8 mm wide; terminal bud scale scars 5–8, prominent, encircling stem. Petiole 8–12 mm long, nonplicate, short in relation to lamina length (9%–11%). Lamina obovate, 10.2–12.5 cm long \times 3.1–3.5 cm wide; margin serrate with regularly spaced rounded, glandular, teeth. Venation pinnate with a straight midvein and 8–15 pairs of brochidodromous secondary veins. Intersecondary veins absent. Tertiary and higher-order veins forming an irregular mesh. Adaxial cuticle smooth, cells polygonal, anticlinal walls straight to slightly curved, almost equally sized, 30–45 μ m in diameter. Abaxial cuticle showing unspecialized cells, straight-walled, stomatal complexes rounded-oval, 35–40 \times 40–50 μ m in diameter, stomatal ledges thick, bordering the broadly oval aperture and not reaching to the poles. Trichome bases lacking on both abaxial and adaxial cuticles.

Holotype. UWBM PB 101336. Specimen bearing both infructescence and leaves (figs. 1A–1E, 2A, 4A). From Boot Hill, Republic, Washington. Burke Museum locality B4131, collected and donated by Dwyane Day in August 1999.

Paratypes. Isolated infructescence from Republic. USNM 537360 from USGS locality 2871, collected by Henry Landis in 1901. Previously figured as *Trochodendron* sp. (fig. 2; fig. 58 in Manchester et al. 2009).

Type locality. Boot Hill, Republic, Ferry County, Washington. UWBM locality B4131, Tom Thumb Ash Member of the Klondike Mountain Formation, latest early Eocene.

Additional locality. McAbee, British Columbia, latest early Eocene.

Other significant specimens. Infructescences from McAbee, British Columbia: TRU L-18 F-636 and counterpart F-637; UWBM PB 101376; UWBM PB 101377; TRU L-18, F-494; UF 18437-70627; leafy twig previously figured as *Trochodendron* by Pigg et al. (2007): TRU 15F428 (fig. 4D); leaves from McAbee: UWBM PB 97820 (fig. 4E); UWBM PB97821 (fig. 4F), UWBM PB 97822 (fig. 4C, 4D in Pigg et al. 2007).

Etymology. The species name recognizes Wesley (“Wes”) Wehr (1929–2004), whose enthusiasm and generosity inspired this work.

Comments. The genus *Concavistylon* was established on the basis of infructescences of *C. kvacekii* from the Miocene of Moose Mountain, Oregon (Manchester et al., 2018). The new species differs by length of pedicels: 3–5 mm in *C. wehrü* versus 2 mm or shorter in *C. kvacekii*. *Concavistylon wehrü* augments our knowledge of this genus with the addition of vegetative characters including phyllotaxy, axillary and terminal buds, terminal bud scale scars, leaf architecture, and epidermal anatomy. The fortuitous discovery of a fossil twig showing attached leaves and fruits from Republic, Washington, provides unequivocal proof that these organs were conspecific. Thus, the *Trochodendron*-like leaves and *Concavistylon* represent the same taxonomic entity. The same kind of fruits and foliage co-occur at McAbee, but we might not have recognized them as conspecific without

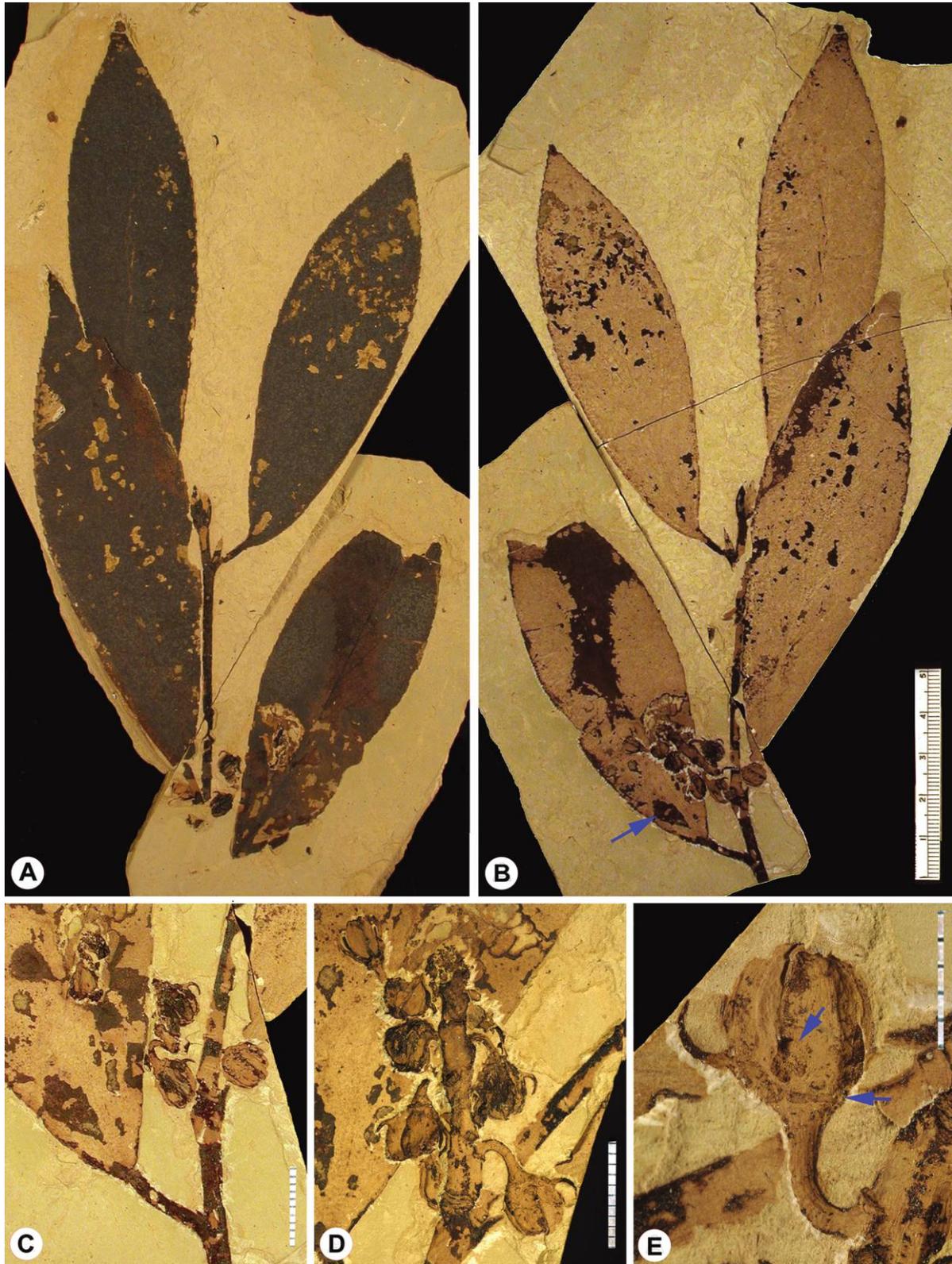


Fig. 1 Holotype of *Concastylon webrii* sp. nov. from Republic, Washington, UWBM PB 101336, by reflected light. *A, B*, Corresponding part-counterpart pieces of twig with attached leaves, buds, and infructescence, with dark residual leaf cuticle adhering mostly on counterpart in *A*. Arrow on *B* indicates patch of adherent cuticle, providing epidermal anatomy by epifluorescence shown in figure 5*B*. *C*, Enlargement from *B*, photographed prior to exposing the physical connection between twig and raceme. *D*, Same region as *C*, after exposing the base of the infructescence and its connection to the twig. Fruits appear pendulous on reproductive axis. Note curved, hornlike persistent styles exposed on some of the fruits. *E*, One of the fruits from *D*, enlarged and rotated, showing one style in side view and another represented as a mold extending into the rock (diagonal arrow), plus scars of perianth at base (horizontal arrow). Scale bars = 5 cm in *B*; 1 cm in *C, D*; and 0.5 cm in *E*.

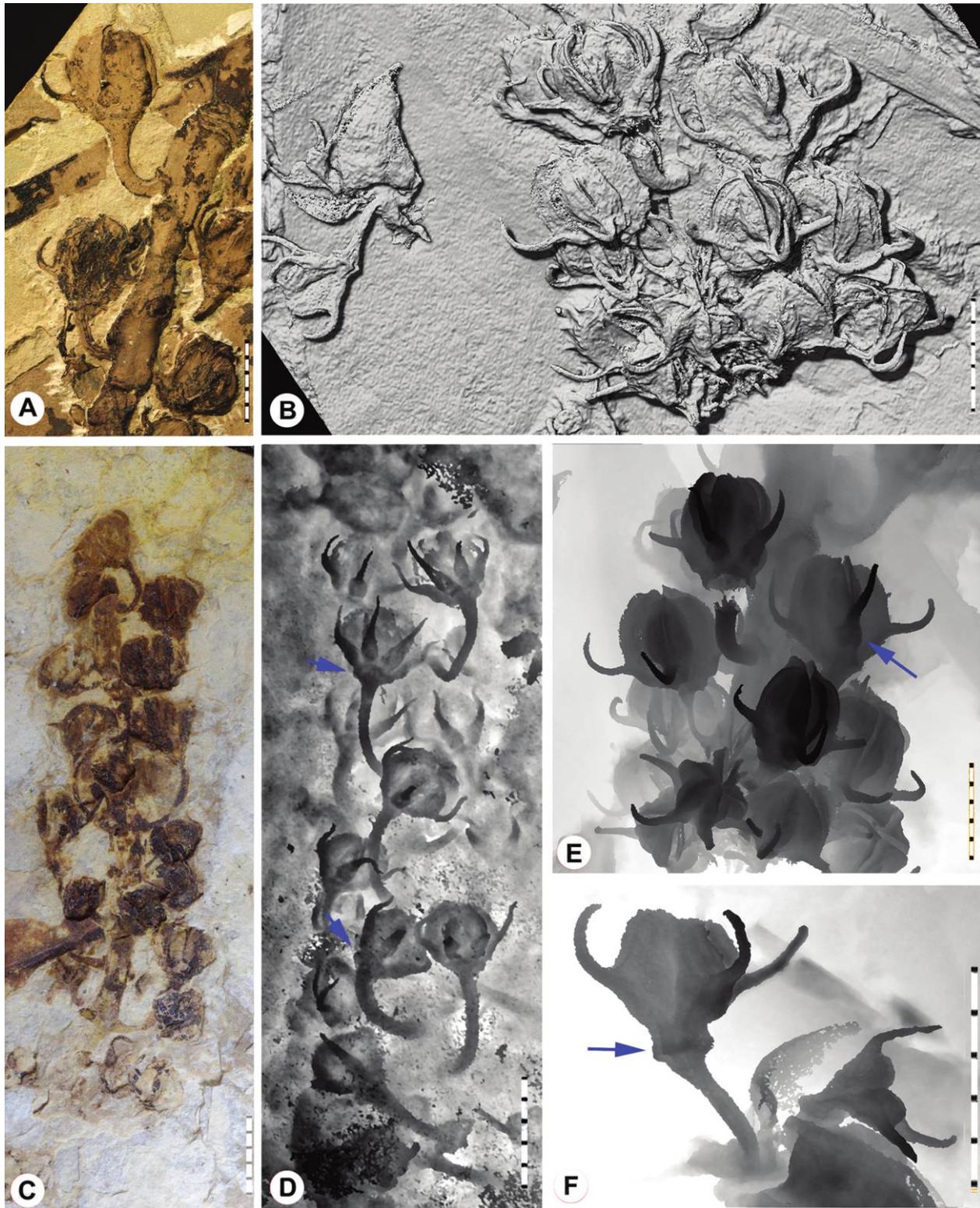


Fig. 2 Infructescences of *Concavistylon webrii*. **A**, Enlargement of holotype (fig. 1) showing connection of infructescence with horizontally oriented terminal bud scale scars at base. Note short, curved pedicles and incurved, hornlike persistent styles, UWBM PB 101336, by reflected light. **B**, Same infructescence viewed through the sediment from behind, showing numerous additional helically attached fruits with subequatorial persistent styles and apically dehiscent capsule valves, micromputed tomography (μ CT) surface rendering. **C**, Isolated raceme from McAbee, British Columbia, showing narrow axis, UWBM PB 101376, reflected light. **D**, Same raceme as in figure 1C, viewed through the sediment from behind, CT, depth mapping. Note up to four styles visible on facing side of each fruit, with symmetry indicating a full complement of four to six styles. Swollen elliptical area basal to each style interpreted as nectary. Note thick disklike structure at fruit base (arrows) interpreted as perianth scar. **E**, **F**, Depth map imagery of the same fruits as in **A**, **B**. **E**, Note swelling beneath each style (arrow) interpreted as nectary. **F**, Fruit showing well-defined styles and scars of the shed perianth (arrow). Scale bars = 5 mm.

the Republic Rosetta Stone specimen. The leaves are borne in alternate phyllotaxy, and the infructescence was borne axillary to a leaf. The twig also shows pointed axillary and terminal buds similar to those seen in extant *Trochodendron* and prominent terminal bud scale scars like those of extant relatives. The McAbee specimen with attached leaves described previously by Pigg et al. (2007, fig. 4A; refigured here, fig. 4D) also shows these features.

Concavistylon wehrlii infructescence axes are straight to somewhat sinuous, 2–3 mm thick at the base, tapering apically to less than 1 mm thick. The longest preserved specimen exceeds 10 cm in length and bears more than 33 helically arranged fruits in a simple raceme (fig. 3G); however, the total length of the infructescence can only be inferred because in all specimens the axis continues beyond the limits of the shale slab that was collected. The holotype shows the basal portion of an infructescence, with an axis 2.6 mm thick, but is broken distally, indicating that the observable length of 2.4 cm is incomplete. The longest infructescence fragment (fig. 3G) is 10 cm long but discontinuous both basally and apically. The thickness of its axis at base and apex are 2.0 and 1.8 mm, respectively, but another increment length of 7 cm is provided by a specimen with a narrower axis (fig. 3F; 1 mm), indicating that it would have been positioned more distally. Logically, the axis is thickest at the base and tapers gradually toward the apex; hence, the lengths of both these specimens can be added indicating an infructescence exceeding 17 cm in length.

The pedicels are 3–5 mm long and about 0.5 mm thick, shorter, and more consistent in length throughout the infructescence than in extant *Trochodendron*. On the basis of the organization and angle of fruit attachment in relation to the infructescence axis, we infer that the axis may have been pendulous with the fruits hanging downward.

Fruits are ovoid to more often slightly obovate loculicidal capsules with a narrow acute base at their point of attachment to the pedicel (figs. 2A–2E, 3). They are 5–6 mm high and 5–7 mm wide with a length-to-width ratio of ca. 0.8–1.3:1. As seen in face view on the compression/impression specimens, many of the fruits show one or two prominent adaxially oriented, hook-like structures protruding from the equator (figs. 1D, 1E, 2A–2E, 3). Prior to recognizing these fossils as Trochodendraceae, we considered the possibility that these structures might represent persistent perianth. However, μ CT scanning of the same specimens clarified their morphology and position and revealed them to be inwardly curved, persistent styles (figs. 2B–2E, 3C, 3D) consistent with those in *Concavistylon kvacekii* from the Miocene of Oregon (Manchester et al., 2018). The μ CT scan imagery reveals 4–6 styles per fruit. Seeds have not been observed, but judging from the apical dehiscence, resembling that of both *Trochodendron* and *Tetracentron*, are likely to have been small winged seeds as in the two modern genera.

An important difference between *Concavistylon* and *Trochodendron* is the presence of an obvious perianth scar at the base of the fruit in the former (fig. 2D, 2F). A prominent perianth does not develop in *Trochodendron* flowers. Although a helix of 3–8 small scales appears during early ontogeny (Hsu et al. 2017), once shed they do not leave discernible scars on the fruit. *Concavistylon wehrlii*, like the type species, *C. kvacekii*, lacks scars of stamens on the infructescences; in contrast, *Trochodendron*

has numerous persistent, protruding staminal scars (text fig. 2F in Manchester et al. 2018).

Concavistylon wehrlii leaves have short petioles both in absolute length (8–12 mm) and in proportion of petiole to lamina length (9%–11%; figs. 1A, 1B, 4D–4F) compared to those of *Trochodendron*. Despite the short petioles, the lamina architecture greatly resembles that of extant *Trochodendron aralioides*, in having pinnate and brochidodromous venation and evenly spaced, rounded, glandular teeth. In some specimens from McAbee, the leaf shows a pair of conspicuous basilaminar extensions (e.g., fig. 4D, 4F; Pigg et al. 2007; fig. 4B, 4E). These have not been found at Republic and are unknown in other extant and fossil Trochodendraceae. In venation, marginal serration, and cuticular anatomy, the leaves having the basal laminar lobes are indistinguishable from the leaves lacking basal laminar lobes.

Leaves of *Concavistylon* were probably thick and evergreen, like those of extant *Trochodendron*, because they are among the rare specimens from the Republic and McAbee localities that preserve cuticles. Cuticle was macerated from the Republic holotype (fig. 5A, 5B) and from McAbee specimens (fig. 5C, 5D). Most other angiosperms from these floras have deciduous leaves and are preserved only as impressions without remnant cuticles. The exception is that leaves of *Trochodendron nastae* from Republic are also preserved with intact cuticle. Our attempts at maceration of the holotype of *C. wehrlii* yielded good results only for the upper epidermis, but epifluorescence revealed portions of the lower epidermis with circular stomata (fig. 5B). *Concavistylon wehrlii* has almost equally sized cells with smooth periclinal walls (fig. 5A, 5C, 5D), while in extant *Trochodendron* the cells are very unequally sized and the outer periclinal wall is domed (fig. 7F, 7G). The stomatal type in the fossil is not easily discerned but corresponds in form, size, and stomatal ledges to the living *Trochodendron*; however, the outer stomatal ring is not seen.

Family—Trochodendraceae Eichler

New genus. *Pentacentron* gen. nov.

Etymology. Referring to the fivefold symmetry of the fruits, contrasting with the consistently tetramerous symmetry of extant *Tetracentron*.

Type species. *Pentacentron sternhartae* sp. n., designated here.

Generic diagnosis. Infructescence a spike of sessile pentacarpellate capsules; raceme axis narrow; capsules subglobose, rounded apically, bearing five persistent styles arising subequatorially and incurved (concave toward fruit apex). Elliptical bulge (interpreted as nectary) beneath each style. Base of fruit with a raised rim representing perianth scars. Dehiscence apical, with separation initiating immediately above each style, and joining apically to form a five-rayed starlike opening.

New species. *Pentacentron sternhartae* sp. nov. (figs. 6A–6G, 7A, 7B).

Etymology. Named for Michael E. Sternberg and Janet L. Hartford, recognizing their promotion of research and education at the Republic fossil site and Stonerose Interpretive Center, Republic, Washington, and whose work facilitated the collection of these specimens.

Holotype. SR 93-08-02, designated here. Collected by Jennifer and David Weber (figs. 6B, 6F–6H, 7C, 7D).

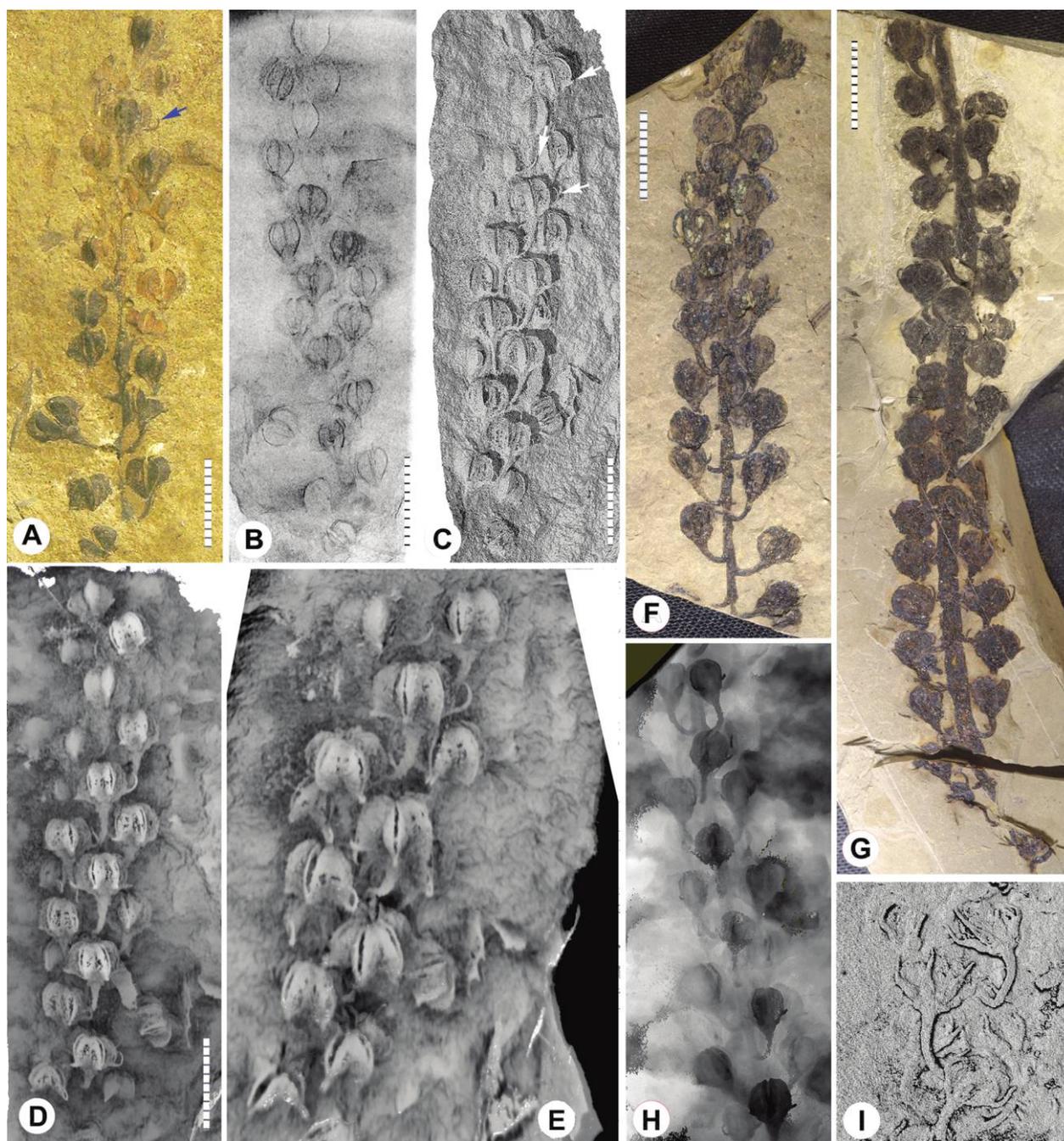


Fig. 3 Infructescences of *Concavistylon webrii*. *A–E*, Raceme from Republic, Washington, USNM 537360 (arrows marking concave persistent styles). *A*, Surface view of shale specimen showing fruits intercepted by longitudinal fracture, reflected light. *B*, Same specimen viewed from behind, with shale rendered translucent, revealing hidden fruits, by micromputed tomography (μ CT) volume rendering. *C*, Surface rendering of the same specimen from μ CT data. *D*, *E*, Same, μ CT depth mapping with detail of fruits with styles (arrows) in lateral and oblique apical view. Note five to six carpellate fruits seen apically. *F*, Raceme from McAbee, British Columbia, with relatively narrow main axis—probably representing apical portion of infructescence, TRU L-18F636, reflected light. *G*, Raceme from McAbee with thicker main axis—probably basal portion, UF18437-70627, reflected light. *H*, Depth map from μ CT scan data for the specimen in *F* (counterpart, TRU L-18 637). *I*, Isosurface rendering of the same specimen as *F*, *H*, showing prominent persistent styles. Scale bars = 1 cm.

Paratypes. SR 06-70-07A, B; SR 07-29-03, SR 10-56-34, SR 10-56-38, SR 11-11-27, SR 11-48-01, SR 11-48-02A, B; SR 11-9-07, designated here.

Type locality. Boot Hill, Republic, Washington. Locality UWBM 4131.

Species description. Infructescences 5.8–9.2 cm long, 0.5–0.8 cm wide, infructescence axis 1.0–2.2 mm thick, bearing helically arranged capsular fruits. Capsules subglobose, pentagonal in apical view, 1.3–4.5 mm wide, styles 1.2 mm long, incurved (convex) toward fruit apex. Elliptical bulge (nectary) beneath

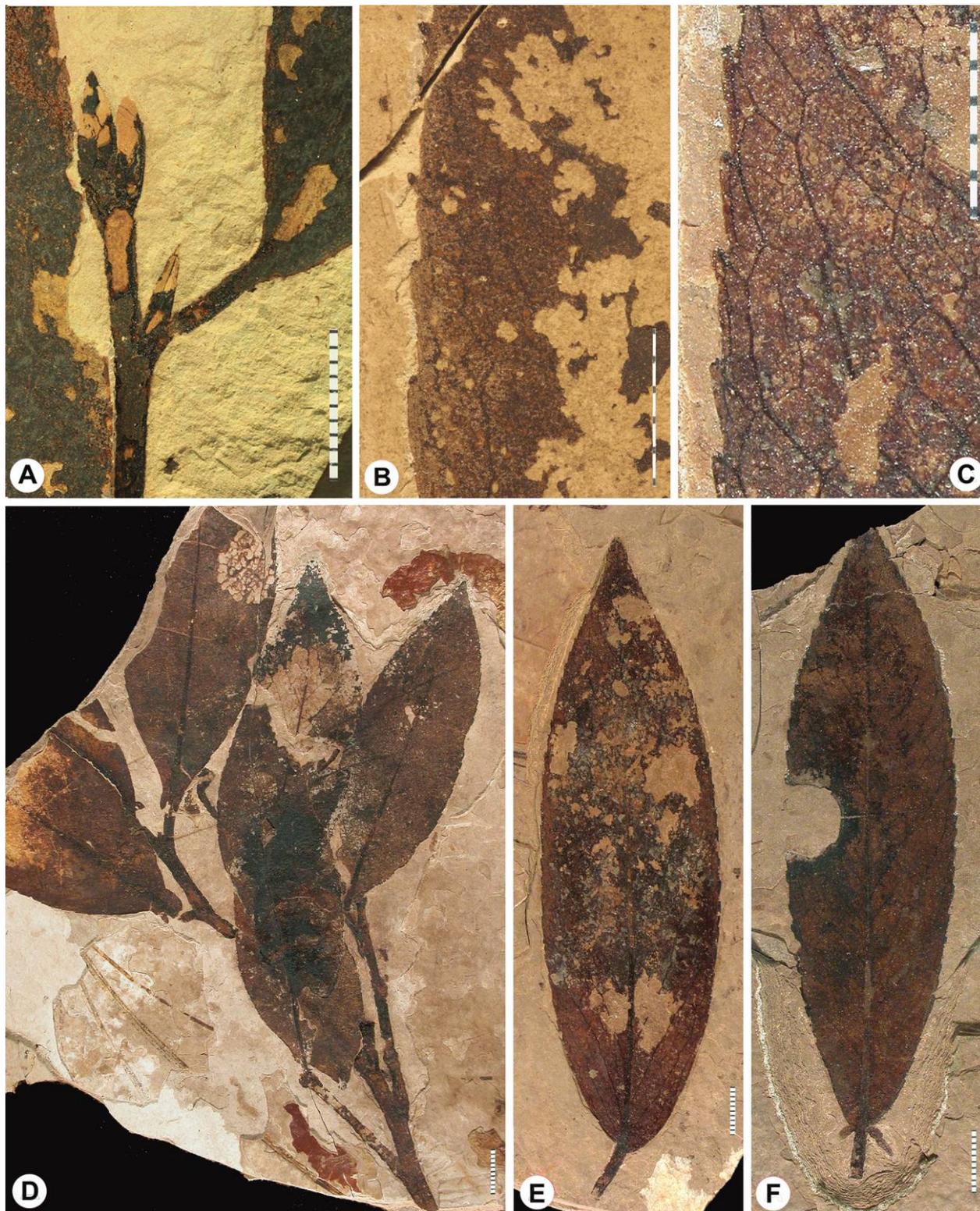


Fig. 4 Vegetative parts of *Concavistylon wehrlii* from Republic, Washington (A, B), and McAbee, British Columbia (C–F). A, Enlargement from figure 1A, showing pointed axillary and terminal buds of the holotype, UWBM PB101336. B, Detail of venation and serrate leaf margin, holotype, UWBM-PB101336. C, Detail of venation and serrate leaf margin, UWBM PB 97820. D, Twig showing alternate phyllotaxy, simple leaves, and short petioles, TRU 15F428. E, F, Isolated leaves including those that yielded cuticle for study of epidermal anatomy. E, UWBM PB 97820. F, Leaf showing basal extensions of lamina and short petiole, UWBM PB 97821. Scale bars = 1 cm in A, D–F, 0.5 cm in B, C.

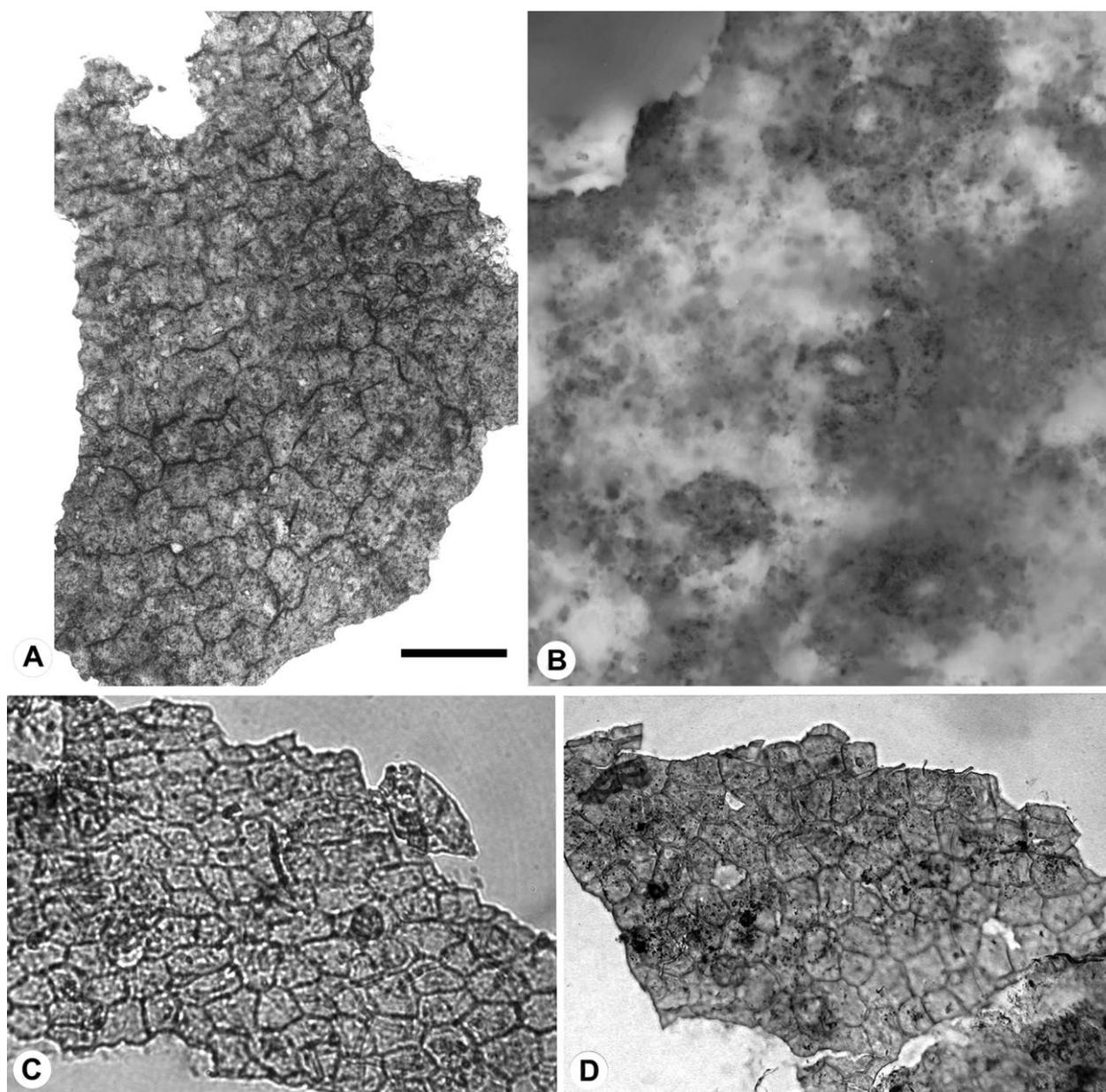


Fig. 5 Cuticles from leaves of *Concavistylon wehrlii* from Republic, Washington (A, B), and McAbee, British Columbia (C, D), transmitted light except as indicated. Adaxial cuticle smooth, cells polygonal, anticlinal walls straight to slightly curved, almost equally sized, 30–45 μm in diameter, UWBM PB 101336. B, Abaxial cuticle from figure 1B by epifluorescence showing unspecialized straight-walled cells and rounded-oval stomatal complexes. C, D, Upper epidermis from leaf in figure 4E, UWBM PB 97820. C, Adaxial cuticle somewhat corroded, cells polygonal, anticlinal walls straight to slightly curved, almost equally sized. D, Adaxial cuticle smooth, cells polygonal, anticlinal walls straight to slightly curved, almost equally sized. Scale bar = 100 μm .

each style 0.4 mm wide, 0.6 mm high. Perianth scar forming a flange beneath each fruit. Capsules dehiscent apically by separation lines extending apically from immediately above each style.

Comments. These spikes and fruits are similar in size, shape, and organization to those of extant *Tetracentron*, but they are consistently five-carpellate (figs. 6, 7A, 7B), rather than tetracarpellate, which is the case in extant (fig. 7C, 7D) and Miocene (Manchester and Chen 2006) infructescences of *Tetracentron*. In contrast to *Tetracentron*, in which the styles are outcurved

(convex, directed away from the fruit axis; fig. 7D, 7E), the styles are usually incurved (concave, directed toward the fruit apex; figs. 6A, 6B, 6F–6H, 7A, 7B), a feature shared with *Concavistylon*.

Although it is not obvious from study of the specimens by reflected light, the μCT imagery reveals the position of perianth at the junction of pedicel and fruit (fig. 6F) as in extant *Tetracentron* (fig. 7C, 7D) and shows a clearly defined nectary pad beneath each style (figs. 6F, 7A). *Tetracentron* also has a nectariferous cavity beneath each style (fig. 7D). Five *Pentacentron* spec-

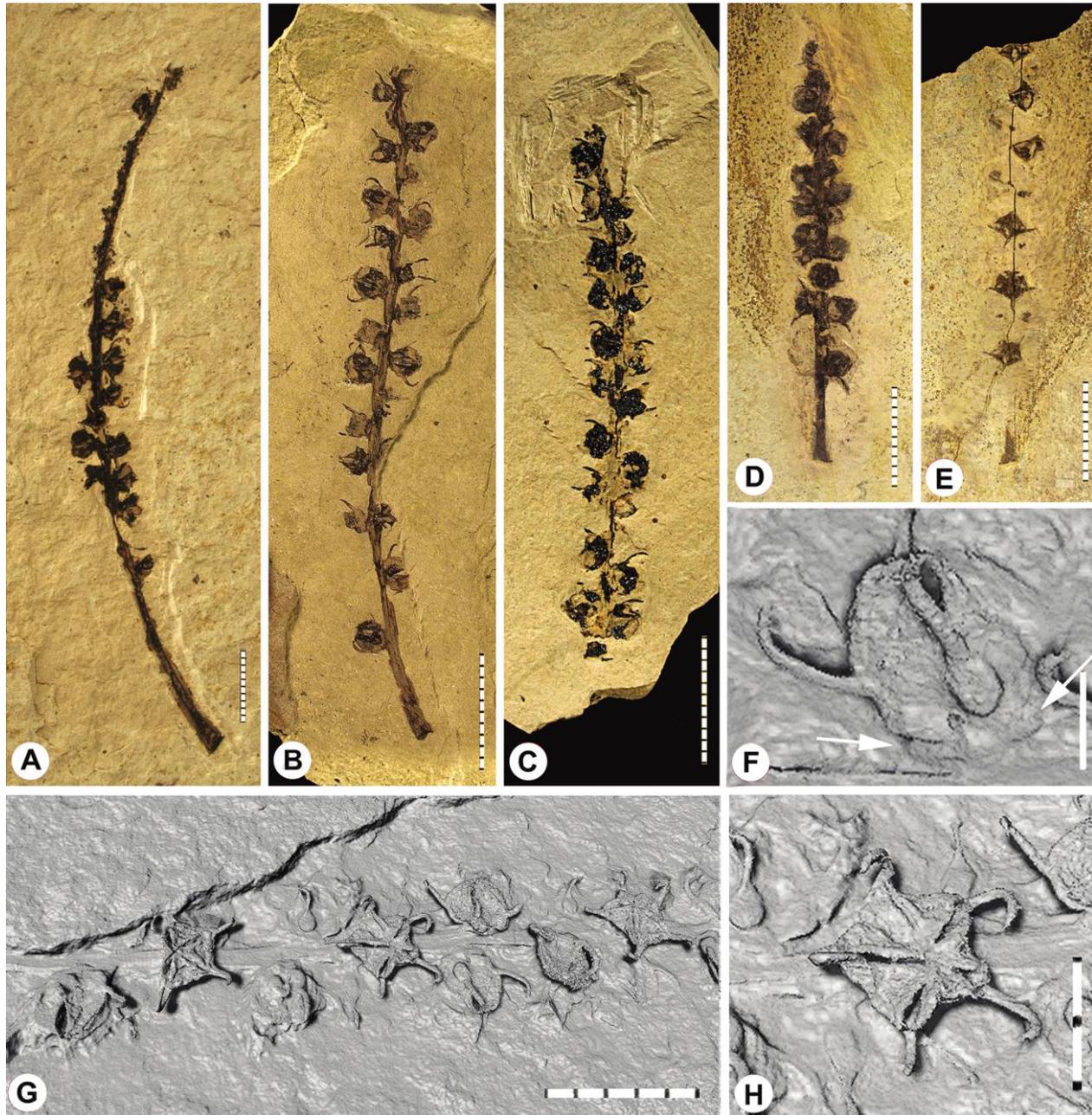


Fig. 6 Infructescences of *Pentacentron sternbartae* gen et. sp. nov. from Republic, Washington. *A*, Longest specimen, showing intact base with many of its fruits shed but several remaining in the middle portion of axis, SR10-56-38. *B*, Holotype showing more than 20 helically arranged fruits, each with prominent persistent styles, SR93-08-2. *C*, Specimen with dark carbonaceous material remaining on many of the fossils, SR10-56-34. *D*, Specimen showing close spacing of fruits and rare outcurved styles on two of the fruits, SR06-70-07A. *E*, Corresponding opposite counterpart of the specimen in *D*, showing five-carpellate fruits in transverse view, SR06-70-07B. *F–H*, Details from the holotype in *B*, micromputed tomography (μ CT). *F*, Single fruit viewed laterally. Note nectary pad beneath styles and position of perianth (arrows), μ CT surface rendering. *G*, Infructescence, oriented horizontally showing pentagonal capsules each with five incurved styles. *H*, Detail of a single fruit in transverse orientation, with apical dehiscence slits aligned with each style. Scale bars = 1 cm in *A–E*; 1 mm in *F*; 5 mm in *G*, *I*, *J*; 2 mm in *H*.

imens were μ CT scanned, and in each case the capsules were seen to be consistently pentamerous. We studied more than 30 fruiting specimens of modern *Tetracentron* in the herbarium in the Kunming Institute of Botany, Chinese Academy of Science, in Yunnan, China (KUN), and several infructescences from a planted

tree in the Washington Park Arboretum in Seattle, and found them to be consistently tetramerous. Fruits of *Pentacentron* are much smaller than those of *Concavistylon*, and this is not attributable to immaturity because in both cases the fruits are at dispersal stage with dehiscence slits gaping and empty of seeds.

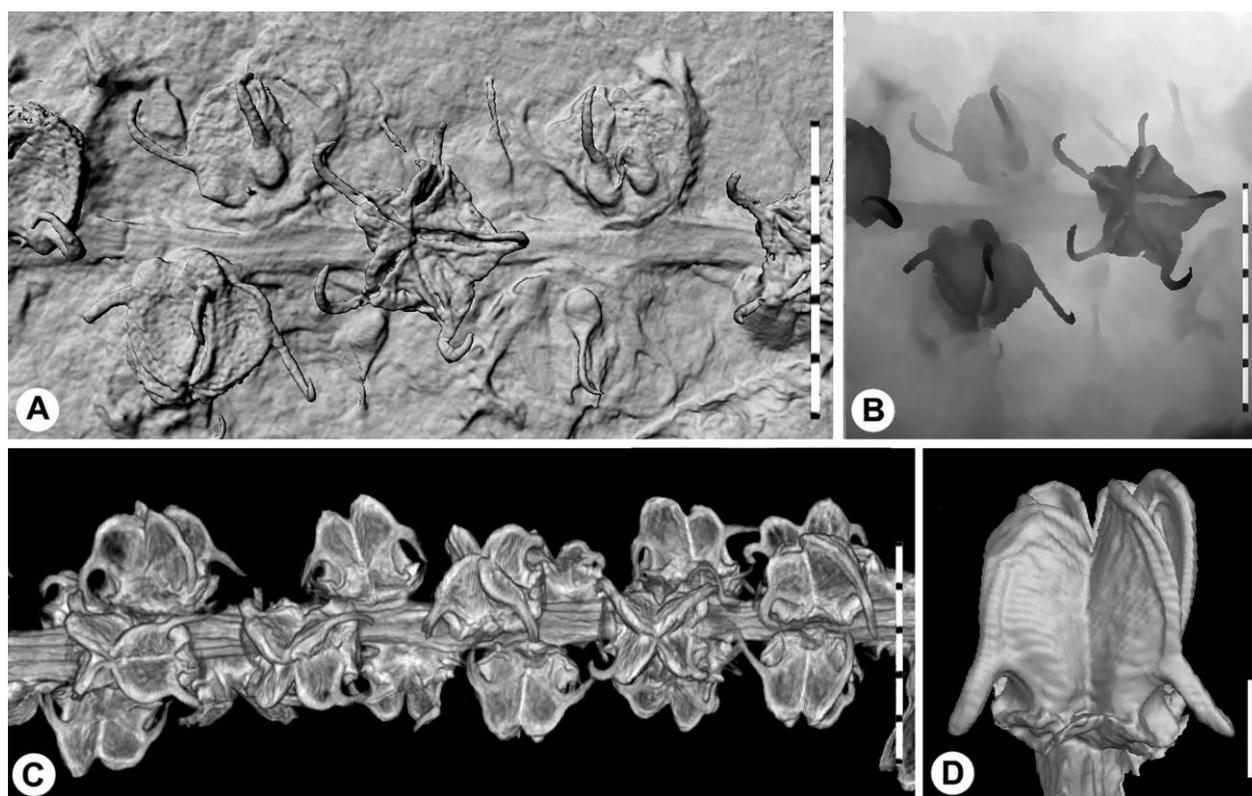


Fig. 7 Infructescences of *Pentacentron sternhartae* and *Tetracentron sinense* Oliv., micromputed tomography surface renderings. **A**, Detail of *P. sternhartae* infructescence, SR06-70-07B. **B**, Depth map image corresponding to middle and left side of **A**, showing upwardly curved (concave) styles and apical dehiscence slits. **C**, Infructescence of *T. sinensis* from Seattle Arboretum, showing tetracarpellate fruits with subtending perianth and outwardly curved (convex) styles. **D**, Fruit showing apical dehiscence and a nectariferous convavity beneath each style. Scale bars = 5 mm in **A–C**; 1 mm in **D**.

For *Pentacentron*, we lack any specimen showing attachment of the infructescence to a leafy twig. Therefore, the corresponding relationships of reproductive structures with leaves remain speculative. However, given the close relationship inferred for *Pentacentron* and *Tetracentron* based on fruit morphology, there is a strong possibility that *Pentacentron* bore leaves more or less identical to those of *Tetracentron*. No fruits conforming in detail to extant *Tetracentron* have been found at the Okanogan Eocene sites, yet they are known to be preservable and recognizable based on Miocene occurrences (Manchester and Chen 2006; Grímsson et al. 2008). Foliage architecturally identical to that of extant

Tetracentron has been recognized from the middle Eocene One Mile Creek locality near Princeton, British Columbia, and assigned to *Tetracentron hopkinsii* (Pigg et al. 2007). Along with the treatment of *T. hopkinsii*, the same authors described and illustrated a single leaf specimen from Republic, which they assigned to *Tetracentron* sp. This specimen lacked preservation of the leaf apex and other details. It was not well enough preserved for the authors to be certain that it was conspecific with *T. hopkinsii* (Pigg et al. 2007). However, additional specimens have confirmed the presence of this species at Republic (K. B. Pigg, personal observation, 2010; SR 02-28-07, SR 07-21-09).

Table 1

Distribution of Trochodendraceae among Eocene Localities of the Okanogan Highlands

	<i>Concavistylon wehrli</i>		<i>Trochodendron nastae</i> leaves	<i>Trochodendron drachbukii</i> fruits	<i>Pentacentron sternhartae</i> fruits	<i>Tetracentron hopkinsii</i> leaves
	Leaves	Fruits				
Republic, WA	++	++	++	?	++	+
McAbee, BC	+	+	+ ^a	++	–	–
One Mile Creek, BC	–	–	–	–	–	++

++ = type locality for the species; + = present; – = not found.

^a Two specimens observed from McAbee: UWBM PB 5686 and UWBM PB 8343.

We would like to know whether *Pentacentron* co-occurred with *T. hopkinsii* at One Mile Creek, but so far no trochodendraceous reproductive structures have been encountered from that site.

Diversity of Trochodendraceae in the Eocene Okanogan Highlands

These new occurrences demonstrate greater diversity among fossil Trochodendraceae than previously recognized. Our assessment of whether the Okanogan Trochodendraceae included

three taxa, or as many as six, is influenced by our concept of how the isolated leaves and fruits corresponded to one another as whole plants. Six entities have been described formally on the basis of leaves, infructescences, or both (table 1): (1) *T. nastae* leaves from Republic (Pigg et al. 2001); (2) *T. drachukii* infructescence from McAbee (Pigg et al. 2007; refigured here, fig. 9); (3) *T. hopkinsii* leaves from Princeton–One Mile Creek (Pigg et al. 2007); (4) *Tetracentron* sp. leaves from Republic (Pigg et al. 2007); which is probably conspecific with *T. hopkinsii* based on subsequently collected specimens from Republic); (5) *C. wehrlii* from

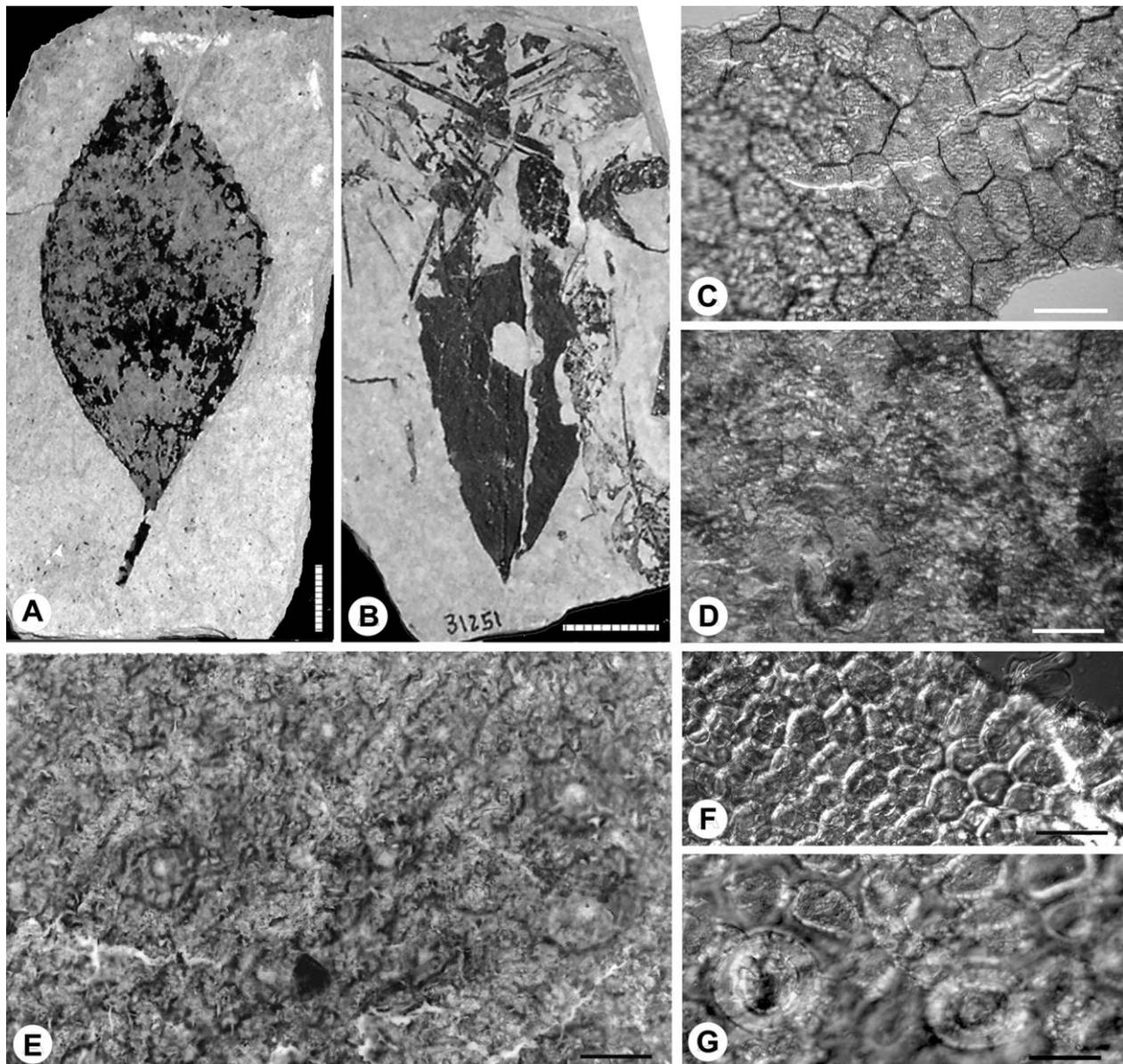


Fig. 8 Fossil *Trochodendron nastae* leaves with cuticle preserved from Republic, Washington (A–E) and extant *Trochodendron aralioides* cuticle (F, G) for comparison. Reflected light except as indicated. A, Specimen showing characteristic palmate venation and finely serrate margin in apical half, SR 98-02-01A. B, Leaf with well-preserved cuticle and poorly preserved venation with faintly visible venation pattern matching that of figure A, UWBM PB 31251. C, Adaxial cuticle from SR 98-02-01A. D, Abaxial cuticle from UWBM PB 31251. E, Abaxial cuticle of UWBM PB 31251 by epifluorescence. F, G, Adaxial and abaxial cuticle of extant *T. aralioides*. Scale bars = 1 cm in A, B; 100 μm in C, E, F; 50 μm in D, G. A color version of this figure is available online.

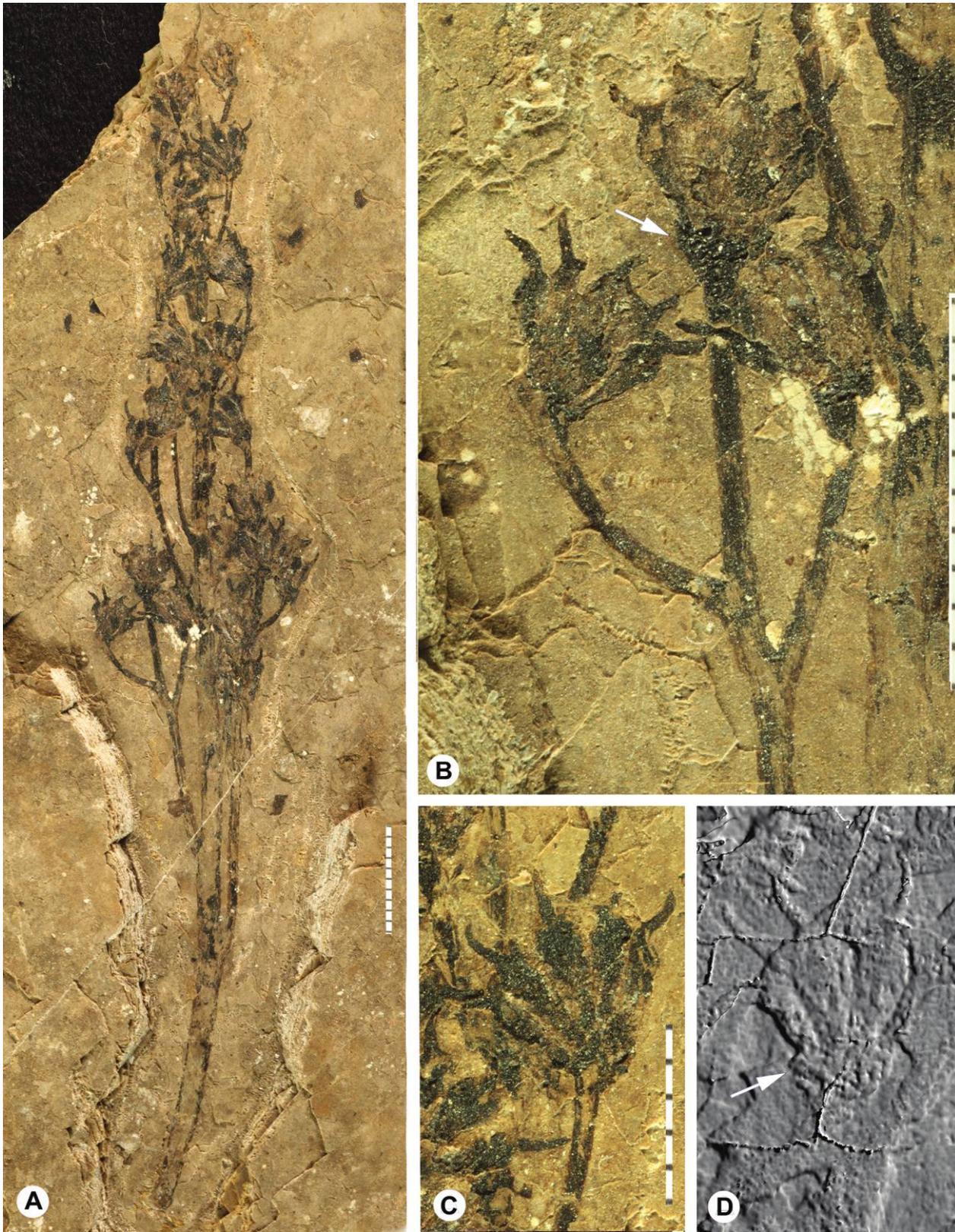


Fig. 9 Fossil *Trochodendron drachukii* Pigg., Dillhoff, DeVore, & Wehr infructescence from McAbee, British Columbia. Holotype, UWBM PB 97819. **A**, Complete panicle. **B**, Detail of pedicellate fruits showing multiple styles and bulge with staminal scars (arrow). **C**, Fruit showing concave styles. **D**, Surface rendering of fruit by microcomputed tomography, showing concave styles and bulge with probable staminal scars (arrow). Scale bars = 1 cm in **A**, **B**; 5 mm in **C**, **D**.

Republic and McAbee, described herein; (6) *P. sternhartae* from Republic, described herein.

Only in the case of *C. wehrlii* do we have proof that leaves and fruits are conspecific due to a specimen preserving their connection on the same twig. There is a reasonable case to be made that the leaves of *T. nastae* (Pigg et al. 2001) were borne by the same kind of plant as *T. drachukii* infructescences (Pigg et al. 2007), although type material of these species is from different localities. There is also a reasonable possibility that the leaves of *T. hopkinsii* or *Tetracentron* sp. of Pigg et al. (2007) were borne by the same plant as the *P. sternhartae* infructescences treated here. If these hypothetical unions are accepted, we arrive at a conservative estimate of three entities: *C. wehrlii*, *T. drachukii*–*T. nastae*, and *P. sternhartae*–*T. hopkinsii* (table 1). In addition, *Nordenskiöldia*, an extinct genus of possible trochodendraceous affinity with records extending from Cretaceous to Miocene, was present in the Eocene of the Okanogan Highlands (Pigg et al. 2001). The assignment of *Nordenskiöldia* to Trochodendraceae was challenged by Doweld (1998) on the basis of differences in infructescence morphology. However, many morphological and anatomical features summarized by Crane et al. (1991), such as homoxyloous wood, favor the placement in or near this family. If *Nordenskiöldia* is accepted as a member of the family, then there were a minimum of four Trochodendraceae in the Okanogan Highlands flora.

Foliar Features of Modern and Fossil Trochodendraceae

Extant *Trochodendron* is characterized by rather coriaceous long-petioled evergreen leaves of variable morphology with pinnate venation and a slightly crenulate margin (Bailey and Nast 1945), and these are similar to Miocene leaves of *Trochodendron evenense* from Kamchatka (Chelebaeva and Chigaeva 1988). Extant *Tetracentron*, in contrast, has chartaceous, deciduous leaves with a fully serrate margin and petioles of moderate length. Eocene *T. nastae* leaves from Republic, Washington, are essentially identical to modern *Trochodendron aralioides*, with the exception of their major venation: they have palmate rather than pinnate basal veins (Wolfe 1989; Pigg et al. 2001). Wolfe (1979) noted that the palmate condition of fossil leaves subsequently named *T. nastae* is shared with *Tetracentron*, despite other architectural differences.

Although cuticle is sometimes preserved in the trochodendraceous leaves from Republic and McAbee, the epidermal anatomy of these fossils' leaves has not been investigated before. We studied epidermal anatomy of *C. wehrlii* leaves as presented in the description above. In addition, we can now augment the description of *T. nastae* with observations of cuticle macerated from specimens from Republic (fig. 8A–8F). Adaxial cuticle is smooth and partly corroded; cells are polygonal and equally sized, with straight to very slightly curved anticlinal walls (fig. 8C). The abaxial cuticle consists of corroded, unspecialized cells with coarsely undulate anticlinal walls, and possibly laterocytic, stomatal complexes with rounded stomatal ledges not reaching to the poles, bordering a widely oval aperture (fig. 7D, 7E). There is no indication of trichome bases on the upper or lower cuticles.

Modern representatives of *Trochodendron* (*Trochodendron aralioides*) and *Tetracentron* (*Tetracentron sinense*) both possess laterocytic stomata (Baranova 1980, 1981, 1983) and rounded stomatal complexes. Both of these extant species, like the fossils

we studied, lack trichomes. The modern species differ from each other by having straight anticlinal walls of unspecialized, unequally sized cells and bulging or domed outer periclinal walls in *Trochodendron* versus smooth cells with undulate anticlinal walls in *Tetracentron*. They also differ in the presence of branched sclereids in mesophyll of *Trochodendron* versus secretory idoblasts in mesophyll of *Tetracentron*. Neither of these features were observed in the fossils. In *Trochodendron*, the stomata show a massive outer stomatal ring (peristomatal rim sensu Wilkinson 1979).

Concavistylon wehrlii infructescences, judging from their thickness at the base, were likely borne erect like those of extant *Trochodendron*, rather than pendulously. The narrow infructescences of *Pentacentron* were probably pendulous like those of extant *Tetracentron*. It is striking that in both of the fossil genera the styles are incurved toward the fruit apex rather than outcurved, contrasting with both species of the two extant genera. Despite the difference in style curvature, these extinct genera exhibit the same peculiar characteristic as the modern members of the family, in that the style bases are displaced outward during fruit development (Endress 1986). Some of the features exhibited in these Eocene fruits might provide insights into pleisiomorphic conditions in the family. Styles of the fossil *T. drachukii* are also mostly concave (fig. 9B–9D). Convex styles, present in the Miocene and extant species of both genera, might be a specialization relative to the concave styles in these extinct genera. Five, rather than four, might have been the ancestral number of carpels in the lineage from which *Tetracentron* originated.

Biogeography

In addition to the Eocene occurrences considered here, *Trochodendron* and *Concavistylon* have been recognized in the Paleocene of Wyoming (Manchester 2018), indicating that western North America was important in the early distribution of the family. Distinctive *Trochodendron*-like pollen has been recognized by combined light microscopy and scanning electron microscopy investigations from the Paleocene of Greenland (Grímsson et al. 2016) and middle Eocene of Germany (Hofman et al. 2018), indicating that the North Atlantic Land Bridge may have been traversed in the early spread of this family. *Concavistylon* is so far unknown outside western North America, but it survived until at least the Miocene (Manchester et al., 2018).

Later occurrences of *Trochodendron*, of Miocene age, are known in western North America (summarized by Manchester et al., 2018), Kamchatka (*Trochodendron kamschaticum* Chelebaeva and Chigaeva infructescence and *Trochodendron evenense* Chelebaeva & Chigaeva leaves; Chelebaeva and Chigaeva 1988), and Japan (Ozaki 1987; Uemura 1988; infructescence figured in Manchester et al. 1991). *Tetracentron* is known from the Middle Miocene of Idaho (infructescences and pollen; Manchester and Chen 2006), Iceland (leaves, pollen, fruits; Grímsson et al. 2008), and Japan (leaves; Suzuki 1967). Clearly, the modern-day distribution centers of these genera are refugial.

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