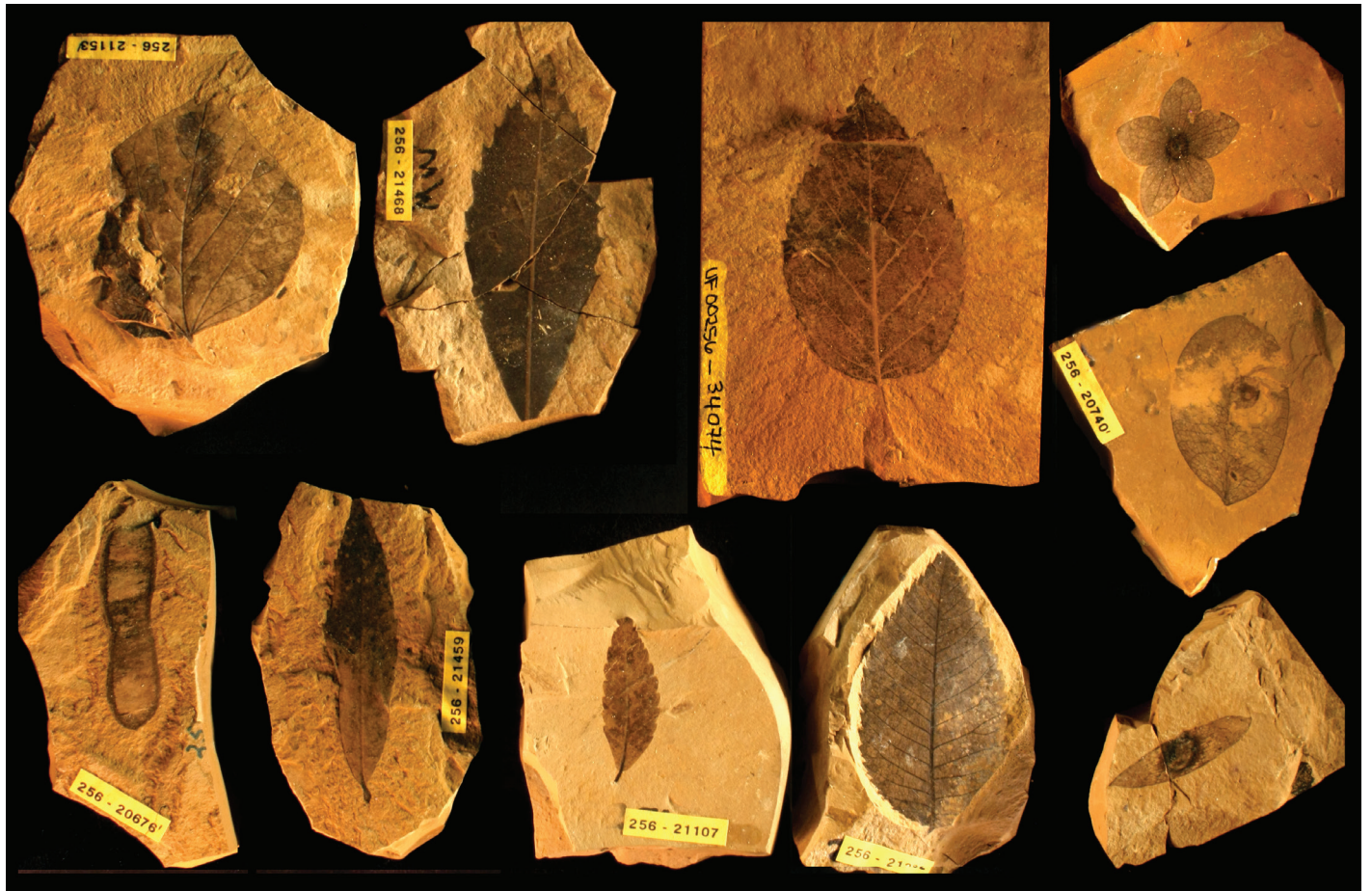


# PaleoBios

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## Steven R. MANCHESTER & Terry A. LOTT (2024). Fossil leaves, fruits and seeds of the Late Eocene Teater Road flora near Post, Oregon, USA.

**Cover:** Selection of representative leaves, flowers and fruits from the Teater Road flora. Top row, left to right: *Cercis*, *Quercus*, *Alnus*, *Florissantia*, and *Koelreuteria*, Bottom row: *Cercis*, *Quercus*, *Cedrelospermum*, *Ulmus*, and *Ailanthus*.

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# Fossil leaves, fruits and seeds of the Late Eocene Teater Road flora near Post, Oregon, USA

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The Teater Road flora, from a small outcrop of lacustrine shale exposed in Late Eocene sediments of the John Day Formation near Post, Oregon, USA, is presented based on abundant, well-preserved leaf and fruit impressions. We recognize 48 genera or morphotypes of leaves and 58 of reproductive structures, with the most abundant representatives including the aquatic fern, *Salvinia*, and a variety of angiosperms including Ulmaceae, Fagaceae, Betulaceae, Malvaceae, Simaroubaceae and Sapindaceae (*Koelreuteria*, *Acer* spp., *Dipteronia*). The Teater Road flora represents a diverse mixed mesophytic assemblage of interest for comparison with other Late Eocene floras of western North America and with the nearby Oligocene Gray Ranch flora. Analyses of foliar physiognomy give estimates of mean annual temperature of ca. 10.4°C and mean annual precipitation of ca. 71 cm per year.

**Keywords:** Teater Road, Eocene, leaves, fruits, angiosperms, paleoecology

## INTRODUCTION

In his book, the Ancient Forests of Oregon, Chaney (1948) provided an overview of paleobotanically-rich Mesozoic and Cenozoic strata giving snapshots of past vegetation and climate change in the Pacific Northwest. In his overview of Cenozoic strata, he included several Eocene floras (Clarno, Comstock and Goshen), a few Oligocene floras (Bridge Creek and Rujada) as well as Neogene floras, notably the Mascall and Deschutes sites. Chaney noticed a remarkable difference between his Eocene floras, which appeared to be tropical, and those of the Oligocene, which indicate temperate hardwood forest. Since Chaney's time, many additional collections have accumulated from both classic localities that he mentioned and from newly discovered localities, offering the potential to examine floristic change through successive intervals of the Early, Middle and Late Eocene.

Recently, an Early Eocene flora has been recognized in the Herren beds of east Birch Creek in northeastern Oregon (Jijina et al. 2019); Middle Eocene shale floras, such as West Branch Creek, mentioned by Chaney (1948), and Cherry Creek (e.g., Hergert 1961) remain to be studied in full. The subtropical Middle Eocene Clarno Nut Beds flora was described with attention to silicified fruits, seeds (Manchester 1994) and woods (Wheeler and Manchester

2002), but the Nut Beds leaf assemblage introduced by Manchester (1981) has not been published in detail.

Late Eocene floras include the John Day Gulch flora of the Clarno Formation (Pl. 14 in Wolfe 1972; although the plate caption does not label the source, all figured specimens of that page are from the John Day Gulch collection now housed at USNM) and the Gray Butte (McFadden 1986, Smith et al. 1998) and Whitecap Knoll (Manchester 2000) floras of the John Day Formation. The Late Eocene floras of Oregon are of interest for comparison both with older and younger floras of the region. Here we provide a comprehensive treatment of the Teater Road flora of Crook County, central Oregon. This flora is from a site in the lower part of the John Day Formation at approximately the same stratigraphic level as the nearby silicified fruit and seed (Manchester and MacIntosh 2007), and wood floras (Wheeler et al. 2006, Wheeler and Manchester 2021), with a radioisotope age of ~36 Ma (Manchester and McIntosh 2007).

The excellent preservation of the Teater Road fossils has led to their incorporation in several studies of individual angiosperm taxa, including *Cedrelospermum* Saporta emend. Manchester (Ulmaceae; Manchester 1987a), *Florissantia* Knowlton emend. Manchester (Malvaceae; Manchester 1992), *Chaneya* Y.-F. Wang and Manchester (Rutaceae/Simaroubaceae; Wang and Manchester 2000),

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*Ailanthus* Desfontaines (Simaroubaceae; Corbett and Manchester 2004), *Acer* spp. (Sapindaceae; Wolfe and Tanai 1987), *Dipteronia* Brown emend. McClain and Manchester (Sapindaceae; McClain and Manchester 2001), *Koelreuteria* Laxmann (Sapindaceae; Wang et al. 2013), and *Cercis* L. (Fabaceae; Jia and Manchester 2014), yet an overview of the flora has not been published. These fossils occur in a diverse warm-temperate assemblage that also includes around 100 other morphotypes (Table 1). Among the Late Eocene floras currently known from north central Oregon, Teater Road has the best preservation of venation details.

### MATERIALS AND METHODS

The Teater Road site (University of Florida locality UF 256) was discovered by Alex Atkins during a paleobotany field program sponsored by the Oregon Museum of Science and Industry in 1984 and was collected periodically over the next few years by teams of high school students led by the first author. Subsequently, local resident paleontologist Melvin S. Ashwill of Madras, Oregon, donated specimens that he collected from the same site to the Florida Museum of Natural History in 2001. Many of the *Acer* L. specimens collected from this site were sent to Jack A. Wolfe for inclusion in a monograph that was published by Wolfe and Tanai (1987); those specimens were deposited at the University of California Museum of Paleontology, Berkeley (UCMP). All other specimens have been deposited at the Florida Museum of Natural History, University of Florida, Gainesville (UF).

The site is located at 44.1666556 N, 120.2488555 W, on the northwest side of Teater Road, 2.7 miles north from Prineville-Paulina Highway in Crook County, Oregon (Fig. 1C in Wheeler et al. 2023). At the time we made our collections this was an access road to the US Forest Service land to the north, but current owners have closed the road. Due to the indurated nature of the shale, it was used for local road gravel projects and the lens has subsequently been exhausted. At present, only small fragments of the shale remain at the site. With the exception of some specimens of *Acer* deposited at UCMP by Jack Wolfe and cited in Wolfe and Tanai (1987), the only collection that we are aware of from Teater Road is housed in the Paleobotanical collections of the Florida Museum of Natural History.

The specimens were collected from a lens of fine-grained shale representing a small lake deposit (Jia and Manchester 2014). The same site was referred to as Sheep Rock Creek by Wolfe and Tanai (1987), but we prefer the local name Teater Road, to avoid confusion with

another more famous geographic feature also known as Sheep Rock situated in Grant County, Oregon (Samuels and Cavin 2013, see fig. 1). The road, indicated by that name on the US Geological Survey Quadrangle maps, was named in reference to the local rancher, Jim Teater.

The Teater Road flora is attributed to the upper Eocene part of the John Day Formation. The age was not determined by direct radiometric dating; however, the site is estimated to be near the same stratigraphic level as the Dietz Hill silicified fruit, seed and wood locality (Wheeler et al. 2023) about 11.5 km due west. That site, UF loc. 278, is immediately below the White Ash of Post (WAP) from which sanidine crystals were obtained that yielded a  $40\text{Ar}/39\text{Ar}$  date of  $36.21 \pm 0.26$  Ma ( $n=26$ ) by the single crystal laser fusion method (Manchester and McIntosh 2007). See Wheeler et al. (2023 fig. 1) for placement of these and other paleobotanical sites on the local geologic map.

Specimens were photographed with a Canon XSI digital camera fitted with a Canon EF 60 or EF100 mm macro lens. Smaller specimens, in the range of 1 to 10 mm, were imaged with a Keyence VHX-7000N digital microscope, using the optical shadow effect mode to accentuate surface topography.

Terminology for leaf description follows Hickey (1973), Radford et al. (1974) and Ellis et al. (2009). Terminology for winged fruit descriptions of *Acer* follows Wolfe and Tanai (1987). Leaves of extant plants from herbaria were used for subsequent fossil/modern comparisons when deemed necessary (Appendix 1). Leaf size categories follow Raunkiaer (1934), Webb (1959) and Ellis et al. (2009), except for the term microphyll which, in paleobotany and plant systematics, refers to a special kind of leaf (with no leaf gap) characteristic of lycopods (not found in seed plants). Thus, we use the term small leaf rather than microphyll. Fossil specimens are numbered with the UF prefix followed by the locality and individual specimen catalog number (e.g., UF 256-21424). Measurements of incomplete leaf specimens were extrapolated based on comparison with complete leaves by length and width estimation. Leaf fragment measurements are based on apical, basal and/or marginal leaf portions that show distinct characters and are not extrapolated to complete leaves due to insufficient material. Fossil specimens were identified to the extent possible on the basis of similarities to extant plants. Similar extant specimens that we investigated are cited by their accession numbers at the herbaria of the University of Florida (FLAS), New York Botanical Garden (NYBG), or the modern reference collection of

the UF Paleobotanical Collection (prefaced UF) (Appendix 1). Climate inferences for Teater Road are based on comparisons with living relatives and analyses of non-monocot angiosperm (“dicot”) leaf physiognomy. Foliar physiognomic calculations for paleoclimate (Appendix 2) included leaf margin analysis (Wolfe 1979, Wing and Greenwood 1993, Wilf 1997, Miller et al. 2006, Peppe et al. 2011) and CLAMP (Climate Leaf Analysis Multivariate Program, Spicer 2011–2024) to infer mean annual temperature and leaf area analysis (Wilf et al. 1998) to infer mean annual precipitation.

### COMPOSITION OF THE FLORA

Table 1 provides a list of megafossil taxa from Teater Road, in phylogenetic sequence according to Soltis et al. (2018). The Teater Road flora includes one species of moss, the aquatic fern, *Salvinia*, two conifers (*Picea*, and *Pinus*) and a predominance of angiosperms. The most diverse family is Sapindaceae, represented by *Koelreuteria*, *Dipteronia* and several species of *Acer*. The most abundant fossils at the site are leaves of *Quercus* (Fagaceae) and *Ulmus* (Ulmaceae), but intensive collecting revealed a great diversity of angiosperms, including Lauraceae (two genera), Ceratophyllaceae, *Smilax* (two species), *Typhoides* and a few other monocots, Berberidaceae (two species of *Mahonia*), Platanaceae, Rosaceae (*Amelanchier* and *Crataegus*), Juglandaceae (*Juglandiphyllites* and *Palaeocarya*), Simaroubaceae (two species), Anacardiaceae (three genera), Betulaceae (two genera), Malvaceae (three genera), Fabaceae (three genera), Hamamelidaceae, Grossulariaceae, Rhamnaceae, Meliaceae, Eucommiaceae, and Oleaceae. Although many of the species can be placed with confidence in extant families and genera, there remain more than 30 morphotypes that are not identified with respect to extant families and genera (Table 1).

The fauna of Teater Road also includes two species of fish scales and one species of the caddisfly larval case, *Terrindusia*.

### SYSTEMATIC PALEONTOLOGY

Systematic classification herein follows Soltis et al. (2018). Authorship of species names for fossil taxa follows LaMotte (1952), Schultze-Motel (2003), and van der Burg (2005, 2006, 2008, 2010, 2011, 2013, 2016). Author names for extant taxa were sourced from Tropicos, GBIF (accessed 2021), and PoWO (accessed 2023). In addition to the formally identified genera presented below, we also assign some of the specimens with unique morphotype numbers, using the prefixes TRL and TRR for Teater Road

Leaf and Teater Road Reproductive, respectively.

BRYOPHYTA SCHIMPER, 1879

HYPNITES ETTINGSHAUSEN, 1853

HYPNITES BROWNII (KIRCHNER) N.G. MILLER, 1980

FIG. 1A

*Hypnites brownii* (Kirchner) Miller, 1980, *The Mosses of North America*, p. 17–18.

**Basionym**—*Hypnum brownii* Kirchner, 1898, *Trans. Acad. Sci. St. Louis* 8, p. 162, 178, pl. XII, figs. 4, 4a.

*Palaeohypnum brownii* (Kirchner) Steere, 1946, *Am. Midl. Nat.* 36, p. 316.

*Archaeomnium brownii* (Kirchner) LaMotte, 1952, *Geol. Soc. Am. Mem.* 51, p. 238.

**Referred specimen**—UF 256-21582.

**Description**—Plant forming a tuft, with lateral extension of stems; width 22 mm, height 14 mm, stems mostly ascending, at least 7 mm long, 0.2 mm wide, and one horizontal stem, forked or nearly opposite; stems naked or with a few linear leaves, leaf length 0.3–0.5 mm; reproductive structures lacking.

**Discussion**—Although size, habit, and branching pattern is moss-like, the lack of capsules precludes precise systematic placement. The Teater Road specimen closely resembles *Hypnites brownii* from the Late Eocene flora of Florissant, Colorado, in the presence of creeping stems that fork or are nearly opposite, with indistinct leaves (Fig. 1A) (Kirchner 1898, MacGinitie 1953, Miller 1980). A similar tufted plant with creeping and erect stems, and thin leaves lying against the stem characterizes the fossil described previously as *Muscites pulvinatus* Saporta (1865) from the Tertiary of France (Saporta 1865) and *Plagiopodopsis cockerelliae* (Britton and Hollick) Steere (1946) from the Florissant flora (Britton and Hollick 1907, Meyer 2003). *Hypnites beckeri* (Steere) N.G. Miller (1980) is another moss found in the late Eocene flora of Metzel Ranch, Montana (Table 2, Becker 1972, Miller 1980, Lielke et al. 2012). Steere (1946) erected a new genus *Palaeohypnum* Steere (1946) and transferred *Hypnum brownii* to *Palaeohypnum brownii* (Steere 1946). LaMotte (1952) stated that *Archaeomnium* Britton (1926) has priority over *Palaeohypnum* and transferred *P. brownii* to *Archaeomnium brownii* (Kirchn.) LaMotte (1952). Miller (1980) then synonymized these species into *Hypnites brownii*.

POLYPODIOPHYTA CRONQUIST, TAKHTAJAN & ZIMMERMANN, 1966

SALVINIALES LINK, 1833

SALVINIACEAE MARTINOV, 1820

**Table 1.** List of megafossil taxa from Teater Road, in phylogenetic sequence according to Soltis et al. (2018). NA=not applicable/unknown.

Division or family	Taxon	Organ	Biome of extant relatives	Figure
Bryophyta	<i>Hypnites brownii</i> (Kirchner) N.G. Miller	whole plant	NA	1A
Salviniaceae	<i>Salvinia</i> sp.	leaf, whole plant	temperate to tropical	1B, C, H
Pinaceae	<i>Pinus</i> sp.	seed	taiga to subtropical	1D, I
	cf. <i>Picea</i> A. Dietrich	seed	taiga to temperate	1E, J
Lauraceae	<i>Laurophyllum eocenicum</i> (Brown) Manchester & Lott n. comb.	leaf	NA	1N
	<i>Daphnogene knowltonii</i> (Meyer & Manchester) Manchester & Lott n. comb.	leaf	NA	1F
Smilacaceae	<i>Smilax</i> cf. <i>rubyensis</i> Becker	leaf	temperate to tropical	1Q
	<i>Smilax</i> sp.	leaf	temperate to tropical	1R
Poales	<i>Typhoides buzekii</i> Meyer & Manchester	leaf	NA	2A
	Morphotype TRL 01	leaf	NA	2B, C
	Morphotype TRL 02	leaf	NA	2D, E
	Morphotype TRL 03	leaf	NA	2F
Ceratophyllaceae	<i>Ceratophyllum</i> sp.	fruit	cosmopolitan	1G
Berberidaceae	<i>Mahonia simplex</i> (Newberry) Arnold	leaflet	temperate	1K
	<i>Mahonia</i> sp. 1	leaflet	temperate	1O, P
Platanaceae	<i>Platanus</i> cf. <i>exaspera</i> Meyer & Manchester	leaf	temperate to subtropical	1S
	<i>Platanus</i> sp.	achene	temperate to subtropical	1M
Hamamelidaceae	cf. <i>Parrotia</i> C.A. Mey.	leaf	mediterranean to subtropical	3Q
Grossulariaceae	<i>Ribes</i> sp.	leaf	taiga to temperate	2G
Malphighiaceae	cf. <i>Heteropterys</i> Kunth		tropical to subtropical	2H
Salicaceae	Morphotype TRL 04	leaf	NA	3R, W
Fabaceae	<i>Cercis herbmeiyeri</i> Jia & Manchester	fruit	temperate to subtropical	2L
	<i>Cercis parvifolia</i> Lesquereux emend. Jia & Manchester	leaf	temperate to subtropical	2M
	cf. <i>Gymnocladus dayana</i> (Knowlton) Chaney & Axelrod	leaflet	temperate	2N
	cf. <i>Gymnocladus hesperia</i> (Brown) MacGinitie	leaflet	temperate	2K
	cf. <i>Acrocarpus</i> R. Wight ex Arnott	fruit	tropical	2Q
	Morphotype TRR 01	fruit	NA	2P, V
	Morphotype TRR 02	fruit	NA	2U

**Table 1 (cont.).** List of megafossil taxa from Teater Road, in phylogenetic sequence according to Soltis et al. (2018). NA=not applicable/unknown.

Division or family	Taxon	Organ	Biome of extant relatives	Figure
Fabaceae	Morphotype TRR 03	fruit	NA	2R
	Morphotype TRL 05	leaflet	NA	2S
	Morphotype TRL 06	leaflet	NA	2O
	Morphotype TRL 07	leaflet	NA	2T
Rhamnaceae	<i>Paliurus favonii</i> Unger	fruit	mediterranean	2W, X
Rosaceae	<i>Amelanchier</i> sp.	leaf	temperate to deserts	3K, L
	cf. <i>Crataegus</i> Tourn. ex. L.	leaf	temperate	3S
	Rosaceous prickly twig	twig	NA	3X
Ulmaceae	<i>Cedrelospermum lineatum</i> (Lesq.) Manchester	fruit	NA	3B
	<i>Cedrelospermum</i> sp.	leaf	NA	3A
	<i>Ulmus chuchuanus</i> (Berry) LaMotte	leaf	temperate to subtropical	3C, D, T
	<i>Ulmus okanaganensis</i> Denk & Dillhoff	leaf, fruit	temperate to subtropical	3E, 3M
	<i>Ulmus</i> sp.	fruit	temperate to subtropical	3N
Betulaceae	<i>Alnus newberryi</i> Meyer & Manchester	leaf	temperate	3F, G, U
	<i>Alnus</i> sp.	infructescence	temperate	3O
	<i>Carpinus</i> sp.	fruit	temperate to subtropical	3P
	Morphotype TRL 08 [ <i>Carpinus</i> / <i>Ostrya</i> ]	leaf	NA	3H, V
	Morphotype TRL 09 [cf. <i>Carpinus</i> ]	leaf	NA	3I, J
Fagaceae	<i>Quercus berryi</i> Trelease	leaf	temperate to tropical	4A, B
	<i>Quercus pollardiana</i> (Knowlton) Axelrod	leaf	NA	4C
	<i>Quercus</i> sp. 1	leaf	NA	4D
	<i>Quercus</i> sp. 2	leaf	NA	4E
	<i>Quercus</i> sp. 3	acorn	NA	7Q
Juglandaceae	<i>Juglandiphyllites cryptatus</i> (Knowlton) Meyer & Manchester	leaf	NA	4H, J
	<i>Palaeocarya</i> sp.	fruit	subtropical to tropical	4G
Lythraceae	<i>Decodon</i> sp.	leaf	temperate	4F, I
Anacardiaceae	<i>Rhus lesquereuxii</i> Meyer & Manchester	leaf	temperate to subtropical	4K
	<i>Toxicodendron</i> sp. 1	infructescence	temperate to tropical	4L
	cf. <i>Toxicodendron</i> Miller	leaf	NA	4M
	<i>Loxopteroides weeksae</i> Manchester & Judd	samara	NA	4N

**Table 1 (cont.).** List of megafossil taxa from Teater Road, in phylogenetic sequence according to Soltis et al. (2018). NA=not applicable/unknown.

Division or family	Taxon	Organ	Biome of extant relatives	Figure
Meliaceae	<i>Cedrela merrillii</i> (Chaney) Brown	seed	tropical	6U
Rutaceae	<i>Rutaspermum</i> sp.	seed	NA	6E
Sapindaceae	<i>Acer clarnoense</i> Wolfe & Tanai emend. Lott & Manchester	leaf	temperate to subtropical	4O, P
	<i>Acer crookense</i> Wolfe & Tanai	samara	temperate to subtropical	5C, D
	<i>Acer meyeri</i> Wolfe & Tanai	samara	temperate to subtropical	5A–C
	<i>Acer oviptrinum</i> Wolfe & Tanai	samara	temperate to subtropical	5E
	<i>Acer postense</i> Wolfe & Tanai	samara	temperate to subtropical	5F, G
	<i>Acer sinuofluviatilis</i> Wolfe & Tanai	samara	temperate to subtropical	5H, I
	<i>Acer</i> sp. 1	leaf	temperate to subtropical	4Q
	<i>Acer</i> sp. 2	samara	temperate to subtropical	5J, K
	<i>Dipteronia brownii</i> McClain & Manchester	fruit	temperate	5L
	cf. <i>Elattostachys</i> (Blume) Radlkofer	leaf	NA	5N
<i>Koelreuteria alleni</i> (Lesq.) Edwards	fruit	temperate	5O	
Simaroubaceae	<i>Ailanthus confucii</i> Unger	fruit	temperate to tropical	5P
	cf. <i>Ailanthus</i> Desfontaines	leaflet	temperate to tropical	6J
Malvaceae	<i>Craigia oregonensis</i> (Arnold) Kvacek, Bužek, & Manchester	valves	temperate to subtropical	6F
	<i>Plafkeris</i> sp.	leaf	NA	6G, H
	<i>Florissantia ashwillii</i> Manchester	fruit	NA	6C
	<i>Florissantia speirii</i> (Lesq.) Manchester	fruit	NA	6D
Hydrangeaceae	<i>Hydrangea</i> sp.	sepal	temperate to tropical	6I
Nyssaceae	<i>Davidia</i> sp.	fruit	temperate	6V
Styracaceae	<i>Flectorivus</i> sp.	leaf	temperate to tropical	6K, L
Eucommiaceae	<i>Eucommia montana</i> Brown	samara	temperate	1L
Oleaceae	<i>Fraxinus</i> sp.	fruit	temperate to subtropical	6P
Incertae sedis	<i>Deviacer wolfei</i> Manchester	samara	NA	6Q
	Morphotype TRL 10	leaf	NA	2I, J
	Morphotype TRR 04	seed	NA	6S, T
	Morphotype TRL 11	leaf	NA	6M
	Morphotype TRL 12 cf Rosaceae	leaf	NA	6A, B

**Table 1 (cont.).** List of megafossil taxa from Teater Road, in phylogenetic sequence according to Soltis et al. (2018). NA=not applicable/unknown.

Division or family	Taxon	Organ	Biome of extant relatives	Figure
Incertae sedis	Morphotype TRL 13	leaf	NA	6N, O
	Morphotype TRR 05	seed	NA	7K
	<i>Chaneya tenuis</i> (Lesquereux) Wang & Manchester	fruit	NA	5Q
Dicotyledoneae Unknown	Morphotype TRR 06	bract	NA	7I
	<i>Antholithes</i> sp.	flower	NA	7A
	<i>Beckerosperma ovalicarpa</i> (Becker) Meyer & Manchester	seed	NA	7L
	Morphotype TRR 07	infructescence	NA	7D, E
	Morphotype TRR 08	drupe	NA	7N
	Morphotype TRR 09	samara	NA	5M
	Morphotype TRR 10	fruit	NA	7R
	Morphotype TRR 11	fruit	NA	7C
	Morphotype TRR 12	infructescence	NA	7F, G
	Morphotype TRR 13	fruit	NA	7H
	Morphotype TRR 14	infructescence	NA	7J
	Morphotype TRR 15	scale	NA	7M
	Morphotype TRR 16	fruit	NA	7O
	Morphotype TRR 17	pyriform structure	NA	7P
	Morphotype TRR 18	seed/fruit	NA	7S
	Morphotype TRR 19	seed	NA	6R
	Morphotype TRL 20	flower	NA	7B

*SALVINIA SÉGUIER, 1754**SALVINIA* SP.

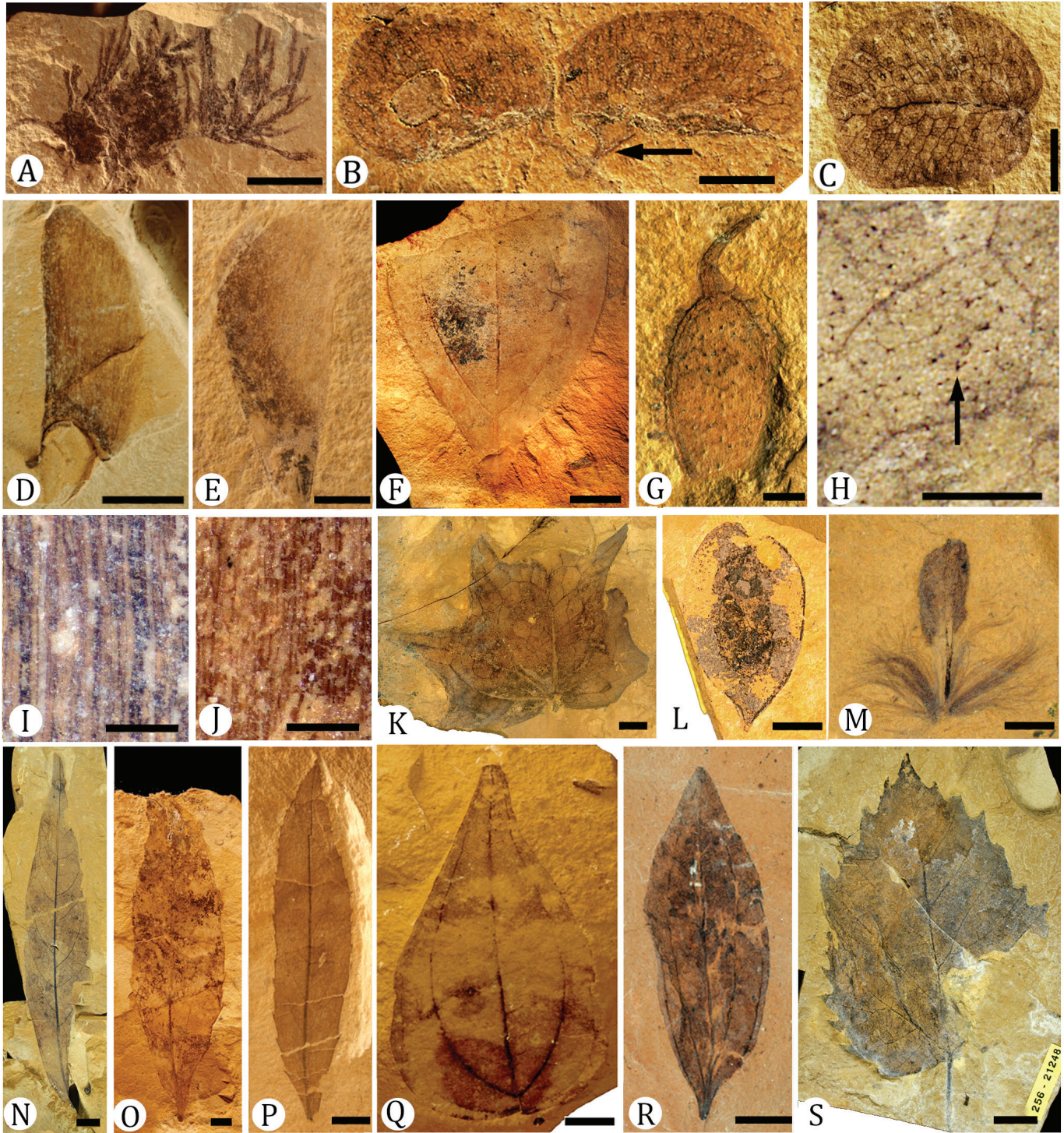
FIG. 1B, 1C, 1H

**Referred specimens**—UF 256-20724b, 20950, 20951a, b, 20952, 20953, 20954a, 20955a, 20956–20959, 20960–20964, 20968–20970, 20973, 20974, 20975a, 20976–20978, 20980, 20982, 20983, 20985–20989a, 20990–20992, 20994–20996a, 20997, 20998a, 20999, 21564a, 21565, 21567a, b, 21568b, 34086a, b, 34088, 79022a, 87097b.

**Description**—Floating leaves recovered mostly as detached, rarely as opposite leaves attached to a non-laminar rhizome-like leaf 5.5 mm long; lamina elliptic or oblate, symmetrical, unlobed, leptophyll or nanophyll, length 5–12 mm ( $\bar{x}$ =7.0, N=47), width 3–8 mm ( $\bar{x}$ =5.0, N=49), l/w ratio 0.9–1.9, leaf area estimate 15–75 mm<sup>2</sup> ( $\bar{x}$ =29, N=45); lamina apex truncate, rounded, or emarginate; base cordate; petiole bifurcate; margin entire;

primary vein single, stout, extending to  $\frac{3}{4}$  leaf length, course zig-zag; secondary venation reticulate, 6–12 per side, angle of divergence for basal pair 114–130°, basal and mid-section 52–76°, apical 42–45°, course zig-zag, very rarely isolated secondary vein to margin; primary areoles quadrilateral to hexagonal, gradually reducing in size towards margin and sometimes with trichomes, each areole with one to rarely two tubercles; tubercles evenly spaced, in rows following course of secondary venation; tertiary veins reticulate, forming secondary areoles.

**Discussion**—Opposite elliptical leaves (Fig. 1B), attached in pairs to a third non laminar submerged root-like leaf (UF 256-34086), and reticulate leaf venation in a zig-zag pattern correspond to extant *Salvinia* (Bierhorst 1971). As an example of a similar extant species, we studied *S. nymphellula* Desveaux (1827), which shares similarities of size, rectangular areoles, and scattered trichomes (Wang et al. 2014, Pérez-Consuegra et al. 2017).



**Figure 1.** **A.** *Hypnites brownii* (Kirchner) Miller, UF 256-21582. **1B, C.** *Salvinia* sp. **B.** Attached, opposite leaves and non-laminar rhizome-like leaf (arrow), UF 256-34086. **C.** Leaf showing reticulate venation, UF 256-20975a. **D.** *Pinus* sp., winged seed, UF 256-20905. **E.** cf. *Picea*, winged seed, UF 256-34113. **F.** *Daphnogene knowltonii* (Meyer and Manchester) n. comb., UF 256-21135. **G.** *Ceratophyllum* sp. fruit with prominent terminal spine, shorter lateral spines and regularly spaced facial protuberances, UF 256-21041. **H.** *Salvinia* sp., detail from C, pentagonal areolae with trichomes (arrow). **I.** *Pinus* sp., enlargement from D, showing wing striation. **J.** cf. *Picea*, enlargement from E showing wing striation. **K.** *Mahonia simplex* (Newberry) Arnold, UF 256-21125. **L.** *Eucomia montana* Brown, samara, UF 256-11051. **M.** *Platanus* sp., achene with basal dispersal hairs, UF 256-20734a. **N.** *Laurophyllum eocenicum* (Brown) n. comb., UF 256-21237'. **O, P.** *Mahonia* sp. 1, UF 256-21547, UF 256-28837. **Q.** *Smilax* cf. *rubyensis* Becker, UF 256-21136. **R.** *Smilax* sp. 1, UF 256-21238. **S.** *Platanus* cf. *exaspera* Meyer and Manchester, UF 256-21248a. Scale bars: **A, D, K, N-R**=5 mm; **B, C, E, L, M**=2 mm; **F, S**=10 mm; **G**=1 mm; **H**=500  $\mu$ m; **I, J**=200  $\mu$ m.

Fossil *Salvinia* foliage has also been recorded from other Eocene sites in Mississippi, Tennessee, Washington, Wyoming, southeastern Nigeria, France, and China (Andrews et al. 1970, Collinson 2001, Wang et al. 2014, Blanchard et al. 2016). In comparison with the Teater Road specimens, *S. elliptica* Newberry (1894) from Washington State, lacks details such as secondary vein arrangement (Hollick 1894). *Salvinia preauriculata* Berry (1925) from western USA, Mississippi and Tennessee differs by its straight secondary veins (Berry 1925, Hickey 1977, Blanchard et al. 2016). *Salvinia aquensis* Saporta (1888) from France is similar in shape, apex, base, and areole shape but has two tubercles per areole (Saporta 1888) rather than predominantly one per areole (Fig. 1H). *Salvinia hainanensis* Jin and Wang (2014) from Hainan Island, China, has opposite secondary vein attachment (Wang et al. 2014). *Salvinia bogotensis* Pérez-Consuegra et al. (2017) from the late Paleocene of Columbia is strikingly similar to our Teater Road specimens in leaf shape, size, apex and base morphology, areole shape, one tubercle per areole, and tubercles in rows following course of secondaries, but the number of secondaries per side is 12–23, rather than 6–12 as observed in our specimens (Pérez-Consuegra et al. 2017).

*Salvinia* is an aquatic fern with about 10–12 species, found mostly in tropical regions of the Americas, Africa, Madagascar, India and southeast Asia, and subtropical regions of the Americas, Asia, and Europe (Nauman 1993, Pérez-Consuegra et al. 2017, PoWO 2023).

GYMNOSPERMAE LINDLEY, 1830

PINALES GOROZHANKIN, 1904

PINACEAE SPRENG. EX RUDOLPHI, 1830

*PINUS* LINNAEUS, 1753

*PINUS* SP.

FIG. 1D, I

**Referred specimen**—UF 256-20905.

**Description**—Seed winged, articulate; single wing extending laterally from seed body, slightly curved and oblong, length 21 mm, width 7 mm; apex obtuse; base acute; proximal margin straight, distal margin convex; wing base extending to 3/4 seed body length on proximal margin in narrow strip, and to 1/3 seed body length on distal margin, both separating from seed body; wing base adjacent to seed body apex with relatively thick, narrow band; wing length 18 mm, width 7 mm; surface with straight, non-undulatory longitudinal striations; seed body outline obovate, length 7 mm, width 4 mm, aligned with wing mid-line.

**Discussion**—Characters of this specimen consistent

with seeds of extant *Pinus* are shape, size, articulation of seed body from the wing, and striations running parallel to the long axis of the wing (Fig. 1I). The detachable seed body is diagnostic of subgenus *Pinus* (syn. *Diploxylon*) (Meyer 2003). Wing striations in Pinaceae are typically undulate (Wolfe and Schorn 1990) as in *Pinus elliotii* Englemann (1880) but can lack undulations as we observed in *P. bungeana* Zuccarini ex. Endlicher (1847). This specimen is similar to *P. macginitlei* Axelrod (1986) specimens that have straight proximal and convex distal margins and a basal distal lobe, such as those identified from the Early Oligocene Beaverhead Basins flora, Montana (Becker 1969, see pl. 6, fig. 5), and to *Pinus* sp. from the Eocene West Branch Creek locality of the Clarno Formation of Oregon (Manchester 1994, see pl. 1, fig. 4), especially the disarticulated seed body (Table 2). *Pinus macginitlei* has also been found in the Late Eocene flora of Ruby Basin, Montana and Florissant flora while *Pinus* sp. in the Late Eocene flora of Gray Butte (Sumner Spring), Oregon, is very similar (Table 2, Axelrod 1986). One of the Teater Road specimens preserves an irregular clump of needles in bundles with a bulbous base attached to a stem with scale scars (UF 256-21583) and is also identified as *Pinus*. Unfortunately, the number of needles per bundle in this specimen, which is important for diagnosing subgroups within *Pinus* (Sargent 1933), is unclear.

*Pinus* subgenus *Pinus* consists of ca. 100 species widely distributed in the Northern Hemisphere, mainly in taiga to temperate regions and tropical mountains (Little and Critchfield 1969, Kral 1993, GBIF 2021).

CF. *PICEA* A. DIETRICH, 1824

FIG. 1E, J

**Referred specimen**—UF 256-34113.

**Description**—Seed winged with a single wing extending laterally from seed body, obovate, symmetrical, length 11 mm, width 5 mm; apex and base rounded; proximal margin straight to 3/4 wing distance then convex to apex, distal margin straight to near apex then arched to apex; wing base narrowly extends along proximal and distal side to ~1/2 seed body length; wing thinning distally; surface with straight, non-undulatory longitudinal striations; seed body obovate, lacking resin vesicles, length 3 mm, width 2 mm, oriented at ~10° angle with wing mid-line.

**Discussion**—This winged seed resembles those of extant *Picea* in size and shape (Fig. 1E), but cone bract morphology would be needed for species confirmation (LePage 2001). According to Wolfe and Schorn (1990), *Picea* seeds are distinct from those of other Pinaceae by

**Table 2.** Comparison of Teater Road and other Eocene and Oligocene macrofossil floras of western United States. Abbreviations: **CO**=Colorado, **MT**=Montana, **OR**=Oregon, **UT**=Utah, **GR**=Green River, **C Fm.**=Clarno Formation, **TR**=Teater Road, **SS**=Summer Spring, **WK**=Whitecap Knoll, **FI**=Florissant, **MC**=Mormon Creek, **MR**=Metzel Ranch, **RB**=Ruby Basin, **YR**=York Ranch, **BB**=Beaverhead Basins, **BC**=Bridge Creek.

Series/Epoch			Middle Eocene		Late Eocene							Early Oligocene		
US State			CO, UT, WY	OR					CO	MT				OR
Division or Family	Genus	Species/Morphotype	GR	C Fm.	TR	SS	WK	FI	MC	MR	RB	YR	BB	BC
Brophyta	<i>Hypnites</i>	<i>H. brownii</i>			X			X						
	<i>Hypnites</i>	<i>H. beckeri</i>								X				
	<i>Plagiopodopsis</i>	<i>P. cockerelliae</i>						X						
Salviniaceae	<i>Salvinia</i>	<i>S. sp.</i>			X									
Pinaceae	<i>Pinus</i>	<i>P. macginitlei</i>						X			X		X	
	<i>Pinus</i>	<i>P. ssp.</i>		X	X	X								
	<i>Picea</i>	<i>P. magna</i>						X					X	
	<i>Picea</i>	<i>P. sp.</i>				X								
	cf. <i>Picea</i>				X									
Lauraceae	<i>Laurophyllum</i>	<i>L. eocenicum</i>	X		X									
	cf. <i>Laurophyllum</i>						X		X					
	<i>Nectandra</i>	<i>N. antillanfolia</i>							X					
	<i>Daphnogene</i>	<i>D. knowltonii</i>			X									X
	<i>Cinnamomophyllum</i>	<i>C. sp.</i>		X		X	X							
	<i>Lindera</i> or <i>Litsea</i>							X				X	X	
Smilacaceae	<i>Smilax</i>	<i>S. labidurommae</i>						X						
		<i>S. cf. rubyensis</i>			X						X			
		<i>S. trinervis</i>												X
		<i>S. sp.</i>			X									
Typhaceae	<i>Typha</i>	<i>T. lesquereuxi</i>						X		X	X	X	X	
		<i>T. sp.</i>				X								
		<i>Typhoides</i>			X									
Poales		Morpotype TRL 01			X									
		Morpotype TRL 02			X									
		Morpotype TRL 03			X									
Ceratophyllaceae	<i>Ceratophyllum</i>	<i>C. sp.</i>	X		X		X							
Berberidaceae	<i>Mahonia</i>	<i>M. simplex</i>			X					X			X	X
		<i>M. subdenticulata</i>						X	X		X		X	
		<i>M. sp.</i>			X	X	X							
Platanaceae	<i>Platanus</i>	<i>P. cf. exaspera</i>			X		X							X
		<i>P. sp. achenes</i>			X		X							X
Hamamelidaceae	cf. <i>Parrotia</i>				X									
	<i>Parrotia</i>	<i>P. brevipetiolata</i>												X
Grossulariaceae	<i>Ribes</i>	<i>R. sp.</i>			X									X
Malphigiaceae	cf. <i>Heteropterys</i>				X									
Salicaceae		Morphotype TRL 04			X									
	<i>Populus</i>	<i>P. payettensis</i>										X	X	
	<i>Salix</i>	<i>S. hesperia</i>								X		X		





**Table 2 (cont.).** Comparison of Teater Road and other Eocene and Oligocene macrofossil floras of western United States. Abbreviations: **CO**=Colorado, **MT**=Montana, **OR**=Oregon, **UT**=Utah, **GR**=Green River, **C Fm.**=Clarno Formation, **TR**=Teater Road, **SS**=Summer Spring, **WK**=Whitecap Knoll, **FI**=Florissant, **MC**=Mormon Creek, **MR**=Metzel Ranch, **RB**=Ruby Basin, **YR**=York Ranch, **BB**=Beaverhead Basins, **BC**=Bridge Creek.

Series/Epoch			Middle Eocene		Late Eocene							Early Oligocene		
US State			CO, UT, WY	OR			CO	MT			OR			
Division or Family	Genus	Species/Morphotype	GR	C Fm.	TR	SS	WK	FI	MC	MR	RB	YR	BB	BC
Anacardiaceae	<i>cf. Toxicodendron</i>				X									
	<i>Loxopteroides</i>	<i>L. weeksae</i>		X	X									
Meliaceae	<i>Cedrela</i>	<i>C. lancifolia</i>						X			X		X	
		<i>C. merrillii</i>			X									X
		<i>C. pteriformis</i>								X			X	
Meliaceae		<i>C. trainii</i>	X											
		<i>C. sp.</i>				X								
Rutaceae	<i>Rutaspermum</i>	<i>R. sp.</i>			X									
Sapindaceae	<i>Acer</i>	<i>A. clarnoense</i>			X									
		<i>A. cranei</i>												X
		<i>A. crookense</i>			X									
		<i>A. meyeri</i>			X									
		<i>A. minor</i>								X			X	
		<i>A. ovipetrinum</i>			X									
		<i>A. postense</i>			X									
		<i>A. sinuofluviatilis</i>			X									
		<i>A. sp. 1</i>			X									
		<i>A. sp. 2</i>			X									
		<i>A. spp.</i>	X			X		X	X		X		X	X
	<i>Dipteronia</i>	<i>D. browni</i>			X	X	X	X			X			
		<i>D. sp.</i>												X
	<i>cf. Elattostachys</i>				X									
	<i>Koelreuteria</i>	<i>K. allenii</i>	X		X			X						
		<i>K. sp.</i>						X		X	X		X	
		<i>K. arnoldi</i>									X		X	
		<i>K. bipinnatoides</i>								X				
		<i>K. mixta</i>							X					
		<i>K. nigricans</i>							X					
Simaroubaceae	<i>Ailanthus</i>	<i>A. americana</i>						X		X	X		X	
		<i>A. confucii</i>			X									
		<i>A. lesquereuxi</i>	X											
		<i>A. sp.</i>			cf.	X	X							
Malvaceae	<i>Craigia</i>	<i>C. oregonensis</i>			X				X				X	X
		<i>C. sp.</i>	X				X				X			
	<i>Plafkeria</i>	<i>P. obliquifolia</i>												X
		<i>P. sp.</i>			X									
	<i>Florissantia</i>	<i>F. ashwillii</i>			X	X	X							
		<i>F. speirii</i>		X	X			X			X		X	X
Hydrangeaceae	<i>Hydrangea</i>	<i>H. californica</i>							X					



**Table 2 (cont.).** Comparison of Teater Road and other Eocene and Oligocene macrofossil floras of western United States. Abbreviations: **CO**=Colorado, **MT**=Montana, **OR**=Oregon, **UT**=Utah, **GR**=Green River, **C Fm.**=Clarno Formation, **TR**=Teater Road, **SS**=Summer Spring, **WK**=Whitecap Knoll, **FI**=Florissant, **MC**=Mormon Creek, **MR**=Metzel Ranch, **RB**=Ruby Basin, **YR**=York Ranch, **BB**=Beaverhead Basins, **BC**=Bridge Creek.

Series/Epoch			Middle Eocene		Late Eocene							Early Oligocene		
US State			CO, UT, WY	OR			CO	MT				OR		
Division or Family	Genus	Species/Morphotype	GR	C. Fm.	TR	SS	WK	FI	MC	MR	RB	YR	BB	BC
		Morphotype TRR 14			X									
		Morphotype TRR 15			X									
		Morphotype TRR 16			X								X	
		Morphotype TRR 17			X									X
		Morphotype TRR 18			X									
		Morphotype TRR 19			X									
		Morphotype TRR 20			X									

the combination of obovate shape, seed typically with an indentation at the base of the proximal margin of the seed body, cellular pattern running parallel to long axis of the wing, and wing lacking constrictions or wrinkling. Our specimen lacks the proximal indentation of the margin, so without additional specimens, we cannot identify this seed type to *Picea* with certainty. In terms of wing striation (Fig. 1J), we cannot distinguish between this specimen from the *Pinus* sp. described above but there are differences in morphology such as seed shape and seed body detachment. The Teater Road specimen resembles those of *Picea magna* MacGinitie (1953) from the Miocene of the Columbia Plateau (Chaney and Axelrod 1959) in its obovate wing, obtuse seed body base, and straight proximal and distal margins at base of the wing, although some specimens have a convexity at the base of the distal wing margin (Wolfe 1964). *Picea magna* has also been found in the Beaverhead Basins and Florissant floras, and a similar *Picea* seed is present in the Sumner Spring flora (Table 2).

*Picea* consists of about 37–40 species of trees distributed in the temperate Northern Hemisphere (Taylor 1993, GBIF 2021, PoWO 2023).

ANGIOSPERMAE LINDLEY, 1830  
 LAURALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820  
 LAURACEAE JUSSIEU, 1789  
 LAUROPHYLLUM GÖPPERT, 1854 EX R.S. HILL 1986  
 LAUROPHYLLUM EOCENICUM (BROWN) N. COMB.

FIG. 1N

*Umbellularia eocenica* Brown, 1940, J. Wash. Acad. Sci.

30(8), p. 350, text-fig. 18.  
*Beilschmiedia eocenica* (Brown) MacGinitie, 1969, Univ. Calif. Publ. Geol. Sci. 83, p. 101–102.

**Referred specimens**—UF 256-21236, 21237, 21544, 21585, 34092.

**Description**—Lamina narrowly elliptic, symmetrical, unlobed, small, length 61–91 mm (x=72, N=3), width 15–22 mm (x=20, N=5), l/w ratio 3.7–4.2, leaf area 663–1359 mm<sup>2</sup> (x=897, N=3), petiole missing; lamina apex and base acute; margin entire; venation pinnate; midvein moderately thick, straight; secondary venation brochidodromous, at least ten pairs, irregular spacing, excurrent attachment, angle of divergence basal 26–40°, middle 40°, apical 40–70°, course smoothly arching, or wavy and losing strength upward, loop length decreasing upward; 0–2 intersecondaries per intercostal area, extending ¾ to leaf margin, course irregular, terminating at tertiaries; tertiary venation predominately reticulate, sometimes percurrent; quaternary venation reticulate; areolation well developed, quadrilateral to pentagonal, some with freely ending veinlets.

**Discussion**—We place these specimens in the morphogenus *Laurophyllum* because of overlap in morphological and anatomical leaf characters among different extant genera, such as *Beilschmiedia* Nees (1831), *Cryptocarya* R. Brown (1810), *Litsea* Lamarck (1792), *Nectandra* Rolander ex Rottboll (1778) and *Ocotea* Aublet (1775), makes it a challenge to identify fossils to a particular modern genus (Kvaček 1971, Worobiec 2003). Characters of our specimens consistent with *Beilschmiedia eocenica* (Brown) MacGinitie (1969) from

the Middle Eocene Green River Formation (MacGinitie 1969) include elliptic leaves with an entire margin, basal secondary angles smaller than upper secondary angles, brochidodromous venation, and fine mesh of tertiary and quaternary veins (Fig. 1N). *Laurophyllum*-like leaves are also found in the Late Eocene floras of Whitecap Knoll and Mormon Creek (*Laurophyllum* or *Nectandra*), Montana, Florissant flora (“*Lindera*”), and Early Oligocene floras of York Ranch and Beaverhead Basins (*Lindera* Thunberg (1763) or *Litsea* Lamarck (1792)) (Table 2). Narrowly elliptic lauraceous leaves seem to be fairly widespread across the Late Eocene to Early Oligocene of the western United States (Table 2) and are widely accepted as indicators for warm and wet conditions (Carpenter et al. 2007).

*DAPHNOGENE* UNGER, 1845

*DAPHNOGENE KNOWLTONII* (MEYER & MANCHESTER, 1997)

N. COMB.

FIG. 1F

*Cinnamomophyllum knowltonii* Meyer and Manchester, 1997, Univ. Calif. Publ. Geol. Sci. 141, p. 68–69, pl. 5, figs. 8, 11.

**Referred specimens**—UF 256-20213, 21130, 21131, 21132a, 21135, 21610.

**Description**—Lamina tending elliptic, symmetrical, unlobed, small, length > 56 mm, width 19–44 mm (x=29, N=6), l/w ratio 2.0–2.6, leaf area estimate 639–890 mm<sup>2</sup> (x=764, N=2), petiole length 7 mm; lamina apex missing; base acute; margin entire; venation pinnate; midvein stout; secondary veins eucamptodromous; pair of opposite, strong secondaries branching above the base, angle of divergence 27–48°, extending to near middle of leaf before weakening and joining superadjacent secondaries; one pair of distally preserved secondaries, angle of divergence 41°; marginal vein present at lamina base; five to six predominantly strong tertiary veins branching from exmedial side of basal secondaries veins, looping with each other to just inside leaf margin; epimedial tertiaries mixed percurrent, acute to the midvein, sinuous to straight; quaternary veins reticulate; areolation well developed, quadrilateral to pentagonal; freely ending veinlets simple.

**Discussion**—Entire-margined leaves with a basal pair of ascending secondary veins (Fig. 1F) characterize many extant Lauraceae, for example, *Aiouea* Aublet (1775), *Cinnamomum* Schäffer (1760), *Nectandra*, *Ocotea*, *Phoebe* Nees (1836), and *Sassafras* J. Presl (1825). These genera can be difficult to distinguish based on leaf architecture alone, so the fossil morphogeneric name *Daphnogene* (syn. *Cinnamomophyllum* Kräusel (1951)) is applied

(Kvaček 1971). While the figured specimen (Fig. 1F) is incomplete, it conforms well to *Cinnamomophyllum knowltonii* Meyer and Manchester (1997) from the Early Oligocene Bridge Creek flora, Oregon (Chaney 1927, Meyer and Manchester 1997) in having a marginal vein, and exmedial looping tertiaries from the basal secondaries. *Daphnogene*-like leaves, sometimes referred to as *Cinnamomophyllum*, also occur in the floras of the Clarno and John Day formations (Table 2). Lauraceae are also represented among the silicified woods from the nearby Dietz Hill locality (Wheeler et al. 2023) (Table 3).

MONOCOTYLEDONES RAY, 1686–1704

LILIALES PERLEB, 1826

SMILACACEAE VENTENAT, 1799

*SMILAX* LINNAEUS, 1753

*SMILAX* CF. *RUBYENSIS* BECKER, 1961

FIG. 1Q

*Smilax rubyensis* Becker, 1961, Geol. Soc. Am. Mem. 82, p. 52–53, Pl. 11, figs. 9–11.

**Referred specimens**—UF 256-21134, 21136, 21235, 21239, 34096, 78821.

**Description**—Lamina ovate, symmetrical, unlobed, small, length 35–42 mm (x=39, N=3), width 16–31 mm (x=21, N=5), l/w ratio 1.6–2.3, leaf area 503–684 mm<sup>2</sup> (x=583, N=3), petiole length 8.5 mm; lamina apex acute; base rounded or truncate; margin entire; midvein moderate, slightly thicker than lateral primaries; primary venation of three basal and one pair of suprabasal acrodromous veins that extend acropetally toward the leaf apex; angle of divergence for basal pair of lateral primaries 21–82°, for suprabasal pair of lateral primaries 10–50°; secondary venation of two basal slightly wavy acrodromous veins extending at least half the lamina length; interior secondaries alternate percurrent, departing from midvein at acute to nearly right angles; tertiary veins reticulate.

**Discussion**—Examples of extant species that are similar to our specimens include *Smilax ocreata* A. de Candolle (1878) and numerous species of *Ripogonum* J.R. Forster and G. Forster (1775) (Ripogonaceae), with a pair of suprabasal acrodromous veins extending to the leaf apex and interior veins, but these acrodromous veins are secondary in *Ripogonum* (Conran et al. 2009, Ding et al. 2011). Our specimens resemble *Smilax rubyensis* from the Ruby Basin flora, in apex, base, and presence of basal and suprabasal acrodromous primary veins (Table 2, Becker 1961, Monroe 1981, Lielke et al. 2012) but our leaf is ovate (Fig. 1Q), not broadly lanceolate as in *S. rubyensis*. Leaves attributed to *Smilax* are also found

**Table 3.** Floristic comparison of Teater Road with Dietz Hill and Post Hammer sites.

Division or Family	Genus	Species/Morphotype	Teater Road	Dietz Hill (UF 278)	Post Hammer (UF 279)
Brophyta	<i>Hypnites</i>	<i>H. brownii</i>	x		
Equisetaceae	<i>Equisetum</i>	<i>E. sp.</i>		x	
Salviniaceae	<i>Salvinia</i>	<i>S. sp.</i>	x		
Palmae	<i>Sabal</i>	<i>S. sp.</i>			x
Taxaceae	<i>Diploporus</i>	<i>D. sp.</i>			x
Pinaceae	<i>Pinus</i>	<i>P. sp.</i>	x		
	<i>Picea</i>	<i>P. sp.</i>	x		
	cf. <i>Picea</i>		x		
Lauraceae				x	
	<i>Laurophyllum</i>	<i>L. eocenicum</i>	x		
	<i>Daphnogene</i>	<i>D. knowltonii</i>	x		
Magnoliaceae	<i>Magnolia</i>	<i>M. sp.</i>		x	
Smilacaceae	<i>Smilax</i>	<i>S. cf. rubyensis</i>	x		
		<i>S. sp.</i>	x		
Typhaceae	<i>Typhoides</i>	<i>T. buzekii</i>	x		
Poales		Morphotype TRL 01	x		
		Morphotype TRL 02	x		
		Morphotype TRL 03	x		
Ceratophyllaceae	<i>Ceratophyllum</i>	<i>C. sp.</i>	x		
Berberidaceae	<i>Mahonia</i>	<i>M. simplex</i>	x		
		<i>M. sp.</i>	x		
Menispermaceae	(Menispermeae)			x	
Platanaceae	<i>Platanus</i>	<i>P. cf. exaspera</i>	x		
		<i>P. sp. achenes</i>	x		
				x	x
Sabiaceae	<i>Sabia</i>	<i>S. sp.</i>		x	
	<i>Meliosma</i>	<i>M. sp.</i>		x	
Hamamelidaceae	cf. <i>Parrotia</i>		x		
Grossulariaceae	<i>Ribes</i>	<i>R. sp.</i>	x		
Malpighiaceae	cf. <i>Heteropterys</i>		x		
Vitaceae	<i>Ampelocissus</i>	<i>A. sp.</i>		x	
	<i>Vitis</i>	<i>V. sp.</i>		x	
Euphorbiaceae				x	
Salicaceae		Morphotype TRL 04	x		
Fabaceae	<i>Cercis</i>	<i>C. herbmeyeri</i>	x		
		<i>C. parvifolia</i>	x		
	cf. <i>Gymnocladus</i>	cf. <i>G. dayana</i>	x		
		cf. <i>G. hesperia</i>	x		
	cf. <i>Acrocarpus</i>		x		
		Morphotype TRR 01	x		
		Morphotype TRL 05	x		
		Morphotype TRR 02	x		

**Table 3 (cont.).** Floristic comparison of Teater Road with Dietz Hill and Post Hammer sites.

Division or Family	Genus	Species/Morphotype	Teater Road	Dietz Hill (UF 278)	Post Hammer (UF 279)
Fabaceae		Morphotype TRR 03	x		
		Morphotype TRL 06	x		
		Morphotype TRL 07			
Cannabaceae	<i>Aphananthe</i>	<i>A. maii</i>		x	
Rhamnaceae	<i>Paliurus</i>	<i>P. favoni</i>	x		
Rosaceae	<i>Amelanchier</i>	<i>A. sp.</i>	x		
	cf. <i>Crataegus</i>	Cf <i>C. sp.</i>	x		
	prickly twig		x		
Ulmaceae	<i>Cedrelospermum</i>	<i>lineatum</i>	x		
		<i>C. sp.</i>	x		
	<i>Ulmus</i>	<i>U. chuchuanus</i>	x		
		<i>U. okanaganensis</i>	x		
		<i>U. sp.</i>	x	x	x
Betulaceae	<i>Alnus</i>	<i>A. newberryi</i>	x		
		<i>A. sp.</i>	x		x
	<i>Asterocarpinus</i>	<i>A. sp.</i>		x	
	<i>Carpinus</i>	<i>C. sp.</i>	x		
		Morphotype TRL 08	x		
	cf. <i>Carpinus</i>	Morphotype TRL 09	x		
	<i>Corylus</i>			x	
Fagaceae	<i>Fagus</i>				x
	<i>Quercus</i>	<i>Q. berryi</i>	x		
		<i>Q. pollardiana</i>	x		
		<i>Q. sp. 1</i>	x		
		<i>Q. sp. 2</i>	x		
		<i>Q. sp. 3</i>	x		
		<i>Q. sp.</i>			x
Juglandaceae	<i>Juglandiphyllites</i>	<i>J. cryptatus</i>	x		
	<i>Carya</i>	<i>J. sp.</i>		x	x
	<i>Palaeocarya</i>	<i>J. sp.</i>	x		
Lythraceae	<i>Decodon</i>	<i>J. sp.</i>	x		
Anacardiaceae	<i>Rhus</i>	<i>R. lesquereuxii</i>	x		
	<i>Toxicodendron</i>	<i>T. sp.</i>	x		
	<i>Pistacia</i>				x
	<i>Loxopteroides</i>	<i>L. weeksae</i>	x		
Burseraceae	<i>Bursericarpum</i>	<i>B. oregonensis</i>		x	
Meliaceae	<i>Cedrela</i>	<i>C. merrillii</i>	x		
		<i>C. sp.</i>		x	
Rutaceae	<i>Rutaspermum</i>	<i>R. sp.</i>	x		
	<i>Zanthoxylum</i>	<i>Z. sp.</i>		x	
Sapindaceae	<i>Acer</i>	<i>A. clarnoense</i>	x		
		<i>A. crookense</i>	x		

**Table 3 (cont.).** Floristic comparison of Teater Road with Dietz Hill and Post Hammer sites.

Division or Family	Genus	Species/Morphotype	Teater Road	Dietz Hill (UF 278)	Post Hammer (UF 279)		
Sapindaceae	<i>Acer</i>	<i>A. meyeri</i>	x				
		<i>A. ovipetrinum</i>	x				
		<i>A. postense</i>	x				
		<i>A. sinuofluviatilis</i>	x				
		<i>A. sp. 1</i>	x				
		<i>A. sp. 2</i>	x				
		<i>A. sp.</i>				x	
	<i>Dipteronia</i>	<i>D. browni</i>	x				
	cf. <i>Elattostachys</i>		x				
	<i>Koelreuteria</i>	<i>K. allenii</i>	x				
Simaroubaceae	<i>Ailanthus</i>	<i>A. confucii</i>	x				
Malvaceae	<i>Craigia</i>	<i>C. oregonensis</i>	x				
		<i>Plafkeria</i>	<i>P. sp.</i>	x			
		<i>Florissantia</i>	<i>F. ashwillii</i>	x			
			<i>F. speirii</i>	x			
Cornales	<i>Alangium</i>			x	x		
	<i>Mastixicarpum</i>	<i>M. occidentale</i>		x	x		
Hydrangeaceae	<i>Hydrangea</i>	<i>H. sp. (sepal)</i>	x				
Nyssaceae	<i>Davidia</i>	<i>D. sp.</i>	x		x		
Styracaceae	<i>Flectorivus</i>	<i>F. sp.</i>	x				
Eucommiaceae	<i>Eucommia</i>	<i>E. montana</i>	x				
Oleaceae	<i>Fraxinus</i>	<i>F. sp.</i>	x				
Incertae Sedis	<i>Deviacer</i>	<i>D. wolfei</i>	x				
		Morphotype TRL 10	x				
		Morphotype TRR 04	x				
		Morphotype TRL 11	x				
		Morphotype TRL 12	x				
		Morphotype TRR 05	x				
		<i>Chaneya</i>	<i>C. tenuis</i>	x			
		Dicotyledoneae unknown		Morphotype TRR 06	x		
				<i>Antholithes</i>	<i>A. sp.</i>	x	
				<i>Beckerosperma</i>	<i>B. ovalicarpa</i>	x	
				Morphotype TRR 07	x		
				Morphotype TRR 08	x		
				Morphotype TRR 09	x		
				Morphotype TRL 13	x		
				Morphotype TRR 10	x		
Morphotype TRR 11	x						
Morphotype TRR 12	x						
	Morphotype TRR 13	x					
	Morphotype TRR 14	x					
	Morphotype TRR 15	x					

**Table 3 (cont.).** Floristic comparison of Teater Road with Dietz Hill and Post Hammer sites.

Division or Family	Genus	Species/Morphotype	Teater Road	Dietz Hill (UF 278)	Post Hammer (UF 279)
Dicotyledoneae unknown		Morphotype TRR 16	x		
		Morphotype TRR 17	x		
		Morphotype TRR 18	x		
		Morphotype TRR 19	x		
		Morphotype TRR 20	x		

in the Florissant and Beaverhead Basins floras, but they do not seem to be widespread in our selected sites of western United States (Table 2). It has been noted that *Smilax*-like leaves could instead be *Dioscorea* Plum. ex L. (1753) (Lielke et al. 2012) but there is a difference in tertiary venation: *S. rubyensis* leaves have reticulate while extant *Dioscorea* leaves have percurrent tertiary venation (Sun et al. 2018). The basal pair of acrodromous veins in UF 21136 could be considered as strong secondary veins, if not weaker primary veins.

*Smilax* consists of 260–300 species of lianas or herbaceous climbers found in tropical to temperate regions (Mabberley 1993, GBIF 2021, PoWO 2023).

SMILAX SP.

FIG. 1R

**Referred specimens**—UF 256-21238, 79036.

**Description**—Lamina elliptic or narrowly elliptic, asymmetrical, unlobed, small, length 29–39 mm ( $x=34$ ,  $N=2$ ), width 10–20 mm ( $x=15$ ,  $N=2$ ), l/w ratio 1.9–2.8, leaf area estimate 225–592 mm<sup>2</sup> ( $x=408$ ,  $N=2$ ), petiole length 4.6 mm; lamina apex acute; base cuneate or rounded; margin entire; midvein moderate, slightly thicker than lateral primaries; primary venation of 3–4 basal acrodromous veins, weaken acropetally to leaf apex, angle of divergence for basal primaries 15–48°; secondary venation of two basal, weak and slightly wavy acrodromous veins, secondary angle of divergence 61°, and extending to near leaf apex; interior secondaries depart midvein at acute to right angles, and are alternate percurrent; higher order venation not preserved.

**Discussion**—This species also resembles *Smilax* and might be a variant of the one described above, differing by its acute (Fig. 1R) rather than an obtuse base. Characters of these specimens are consistent with extant Smilacaceae and Dioscoreaceae in the presence of only basal primary acrodromous venation, and interior

secondaries; however, in Dioscoreaceae (e.g., *Dioscorea bulbifera* L., 1753), the interior veins are distinctly opposite percurrent (Dilcher and Lott 2005). This species differs from *Smilax labidurommae* Cockerell (1914) of the Florissant flora which has a more broadly ovate leaf (MacGinitie 1953, Manchester 2001). *Smilax lamarensis* Knowlton (1899) as reported from the Miocene Latah Formation of eastern Washington and northwestern Idaho differs by its interior secondaries (Berry 1929).

POALES SMALL, 1903

TYPHOIDES MEYER & MANCHESTER, 1997

TYPHOIDES BUZEKII MEYER & MANCHESTER, 1997

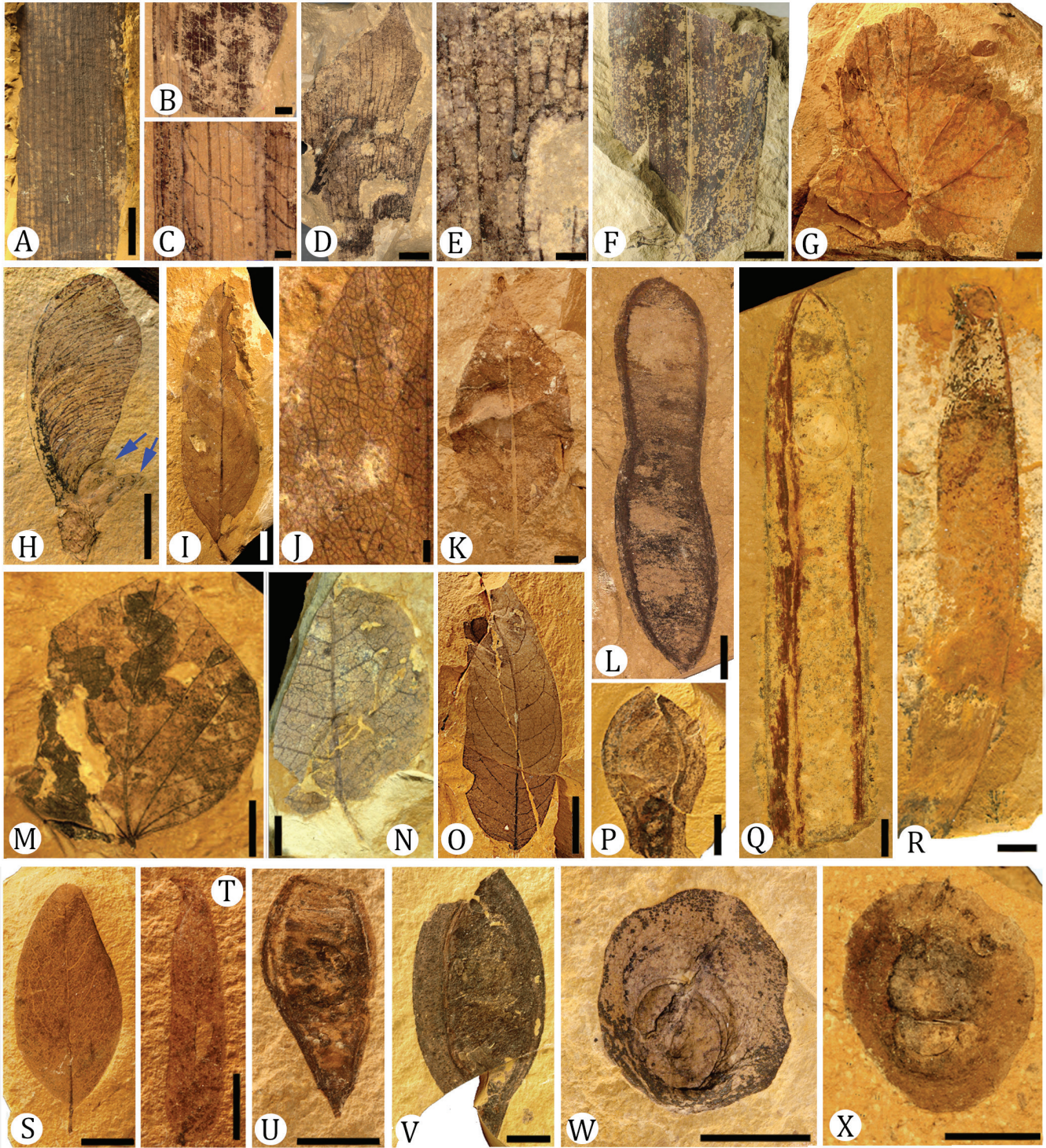
FIG. 2A

*Typhoides buzekii* Meyer and Manchester, 1997, Univ. Cal. Pub. Geol. Sci. 141, p. 159, pl. 73, figs. 1–3.

**Referred specimens**—UF 256-20680b, 21152b, 21227, 21228, 21230, 21231, 21508b.

**Description**—Lamina linear with parallel margins, length > 90 mm, width 3–23 mm ( $x=12$ ,  $N=8$ ); venation with 2–3 orders of parallel veins, no differentiated midvein; cross veins straight and at right angles to long axis of leaf, traversing between adjacent thick veins.

**Discussion**—These specimens are consistent with the leaf architecture of extant *Typha* L. (1753) and *Sparganium* L. (1753). Because these genera cannot be distinguished on leaf architecture alone, we place these leaves in the fossil genus *Typhoides*. The lack of reproductive structures or leaf anatomy precludes a more precise systematic placement. These specimens conform with *Typhoides buzekii* from the Bridge Creek flora (Meyer and Manchester 1997) in having 2–3 orders of parallel veins, lacking a midrib, and having similar cross venation (Fig. 2A). The descriptions and discussion for *Typha lesquereuxi* Cockerell (1906) leaves found in Metzel Ranch, Ruby Basin, York Ranch, Beaverhead Basins and Florissant floras suggests that they may also represent



**Figure 2.** A. *Typhoides buzekii* Meyer and Manchester, UF 256-21228; B, C. Morphotype TRL 01 Monocot leaf fragment with diagonal cross veins, UF 256-46611. D, E. Morphotype TRL 02, monocot leaf, UF 256-17169. F. Morphotype TRL 03, palm or grass leaf, UF 256-21229. G. *Ribes* sp., UF 256-21241. H. cf. *Heteropterys* H.B.K winged fruit of Malpighiaceae, UF 256-20846. I, J. Morphotype TRL 10. Possible legume leaflet with detail of higher order venation, UF 256-21387. K. cf. *Gymnocladus hesperia* (Brown) MacGinitie, UF 256-21082. L. Pod of *Cercis herbmeyeri* Jia and Manchester, UF 256-20676a. M. Leaf of *Cercis parvifolia* Lesquereux, UF 256-21153 N. Leaf of *Gymnocladus dayana* (Knowlton) Chaney and Axelrod, UF 256-UF 21073. O. Morphotype TRL 06, UF 256-21546a. P. Morphotype TRR 01. Pod with pronounced sutural wing, UF 256-20695a. Q. cf. *Acrocarpus* sp., legume pod, UF 256-34079a. R. Pod. Morphotype TRR 03, UF 256-20681. S. Morphotype TRL 05, legume leaflet, UF 256-21441. T. Morphotype TRL 07, legume leaflet, UF 256-20804. U. Morphotype TRR 02, legume pod, UF 256-34104. V. Morphotype TRR 01. Pod with pronounced sutural wing, UF 256-20695b. W. *Paliurus favonii* Unger, winged fruit, UF 256-21060. X. *P. favonii* Unger, winged fruit, UF 256-34103. Scale bars: A, O=10 mm; B=2 mm; C, E, J=1 mm; D, F, G, I, K-N, P-S, U-X=5 mm; H=4 mm; T=3 mm.

*Typhoides* (MacGinitie 1953, Becker 1961, 1969, 1972, 1973). *Typha* sp. (which may instead represent *Typhoides*) is also found in the Sumner Spring flora (Table 2).

*Typha* includes 10–40 extant species that are aquatic, growing in shallow waters, and are cosmopolitan in distribution (Mabberley 1993, GBIF 2021, PoWO 2023). *Sparganium* includes 12 species, also aquatic, distributed in North Temperate regions plus Malesia to Australia and New Zealand (Mabberley 1993).

MORPHOTYPE TRL 01

FIG. 2B, C

**Referred specimens**—UF 256-46611.

**Description**—Lamina linear, available incomplete fragment 14 mm long, 16 mm wide. Margin entire, venation parallel, apparently without distinct midvein; having three orders of alternating thickness: stronger, intermediate and weaker veins; stronger sets of veins about 2 mm apart; cross veins prominent, running uninterrupted, diagonally across the sets of parallel veins.

**Discussion**—Although fragmentary, the pattern of venation is distinct from that of other monocots in the Teater Road flora. We have not conducted a thorough comparative study, but similar venation patterns occur in some extant genera of Arecaceae and Cyclanthaceae (S.Y. Smith, pers. comm., March 2024).

MORPHOTYPE TRL 02

FIG. 2D, E

**Referred specimens**—UF 256-17169, 21233, 20676b, 84599.

**Description**—Lamina elongate, incomplete, length > 95 mm, width 5–19 mm ( $x=11$ ,  $N=4$ ); venation parallel, of one order, no differentiated midvein; closely spaced transverse cross veins connect adjacent longitudinal veins.

**Discussion**—Morphotype TRL 2 (Fig. 2D) may be linear leaves or fragments of much larger leaves torn along the parallel veins. Similar venation can be found in linear leaves of extant Poaceae, in larger leaves of some extant Liliaceae, and extinct *Zingiberopsis isonervosa* Hickey (1962) from the late Paleocene of North Dakota, and the Early Eocene of North Dakota and Wyoming (Hickey and Peterson 1978). Cuticular characters would be needed to verify if they are of graminoid affinity (Conwentz 1886, Litke 1968).

MORPHOTYPE TRL 03

FIG. 2F

**Referred specimen**—UF 256-21229.

**Description**—Lamina segment linear, length >38 mm, width 21 mm; lamina apex and base missing; margin entire; venation parallel with a well differentiated midvein and two orders of fine parallel veins; cross veins not evident.

**Discussion**—This strap-like leaf (Fig. 2F) with a well defined midvein and parallel venation may belong to the palm form genus *Amesoneuron* Goeppert (1852) (Read and Hickey 1972) but it could alternatively be a species of grass. *Amesoneuron* is rarely recorded in extinct floras of North America (Wilf et al. 1998), possibly due to the nature of indistinct palm-like leaf fragments; when more complete leaves are available, they can often be attributed to other genera (Read and Hickey 1972).

CERATOPHYLLACEAE GRAY, 1822

*CERATOPHYLLUM* SP.

FIG. 1G

**Referred specimen**—UF 256-21041.

**Description**—Elliptical fruit with long terminal spine, closely spaced lateral spines and regularly spaced short facial spines; fruit length 5.8 mm, width 3.5 mm; stylar spine length 2.2 mm, width 1.0 mm; apex and base of endocarp rounded; distinct; surface with faint, closely spaced longitudinal striations and random indentations marking spine bases.

**Discussion**—This fruit closely resembles that of the aquatic angiosperm, *Ceratophyllum* L. (1753). Extant *C. murcatum* Chamisso (1829) can produce very similar fruits (Les 1988). Fruits of this genus have also been recognized from the Late Eocene Whitecap Knoll site (Manchester 2000) as well as the Green River Formation (Table 2, Herendeen et al. 1990).

RANUNCULALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820

BERBERIDACEAE JUSSIEU, 1789

*MAHONIA* NUTTALL, 1818

*MAHONIA SIMPLEX* (NEWBERRY) ARNOLD, 1936 A

FIG. 1K

*Mahonia simplex* (Newberry) Arnold, 1936a, *pro parte*, Univ. Mich. Contrib. Mus. Paleont. 5, p. 58–61.

*Berberis simplex* Newberry, 1883, U.S. Nat. Mus. Proc. 5, p. 514.

**Referred specimens**—UF 256-21124, 21125.

**Description**—Leaflet subcircular or ovate, asymmetrical, unlobed, small, length 33–40 mm ( $x=36$ ,  $N=2$ ), width 33–48 mm ( $x=41$ ,  $N=2$ ), l/w ratio 0.8–1, leaflet area estimate 717–1289 mm<sup>2</sup> ( $x=1003$ ,  $N=2$ ), petiolule missing; lamina apex acute; base rounded to slightly cordate; margin prominently toothed, with 2–3 triangular spinose

teeth per side, 6.6–11.4 mm in length, apical tooth longer, 15 mm in length, apex acute; teeth with a pair of tertiary veins parallel to margin but merging into margin before reaching tooth apices; primary venation basal actinodromous, with basal pair of primary veins looping upwards to greater than ½ leaf length and joining secondary veins; secondary venation pinnate, craspedodromous with straight to sinuous course, or semicraspedodromous; tertiary and quaternary venation reticulate; marginal vein present.

**Discussion**—The Teater Road specimens conform to *Mahonia simplex* a species first recognized based on compound leaves and leaflets from Bridge Creek and subsequently identified from sites such as Metzel Ranch and Beaverhead Basins floras (Table 2), the Oligocene site of Haynes Creek, and Miocene sites including Succor Creek and Mascall. They share a subcircular leaflet with a subcordate base, palmate basal venation and large teeth (Fig. 1K). These characters indicate that the species belongs to the Group Orientale of *Mahonia* which has one extant species in western North America and many in eastern Asia (Schorn 1966, Meyer and Manchester 1997, Chen et al. 2020). The Asian species, *Berberis oiwakensis* (Hayata) Laferr. (1997) (syn. *Mahonia lomariifolia* Takeda, 1917) is one of the comparable extant species, sharing characters of palmate venation, and the number and size of the teeth (Ramírez and Cervillos-Ferriz 2000).

*Mahonia* has an excellent fossil record in the Northern Hemisphere that has been summarized by Güner and Denk (2012). In their review, Güner and Denk (2012) noted that some of the specimens previously attributed to Newberry's fossil species, *M. simplex*, do not conform strictly to that species, and the name has been used inadvertently to accommodate specimens that belong in both the extant groups Orientales and Occidentales. One of the specimens placed in *M. simplex* by Meyer and Manchester (1997, see pl. 6, fig. 7) and some of those illustrated by Arnold (1936a, see pl. 1, figs. 6, 7) are now placed in *M. grimmii* Güner and Denk (2012) which are closely similar to the Group Occidentales because of the strong midvein, rather than basally palmate primary veins, and more prominent marginal looping. Although *Mahonia* Group Orientales is disjunct today between western North America and eastern Asia, it was present in Europe during the Miocene (Güner and Denk 2012) as well as Asia (Huang et al. 2016, Hu et al. 2017).

Some of the species formerly placed in *Mahonia* (namely the Horridus group) have been transferred to a separate genus, *Alloberberis* C.C. Yu and K.F. Chung (2017), based on molecular data in order to maintain

monophyly of the genera *Berberis* L. and *Mahonia* (Yu and Chung 2017, Chen et al. 2020).

The Teater Road specimens conform to *M. simplex* as it is known from the type material. They are also similar to *M. marginata* (Lesquereux) Arnold (1936a) from Florissant (MacGinitie 1953: pl. 16, fig. 6), but in *M. marginata* the basal actinodromous veins extend closer to the lamina apex. The distinctly craspedodromous secondary veins support *M. marginata* to be close to Group Occidentales of *Mahonia*, whereas secondary veins forming a series of loops are similar to those of species in Group Orientales.

*Mahonia* consists of about 100 species of shrubs or treelets in temperate or chaparral biomes, distributed from eastern Asia through Sumatra and in North and Central America (Mabberley 1993, GBIF 2021).

MAHONIA SP.

FIG. 10, P

**Referred specimens**—UF 256-21515, 21547, 21608, 28837.

**Description**—Leaflet elliptic, symmetrical, unlobed, small, length 45–93 mm ( $x=70$ ,  $N=3$ ), width 10–23 mm ( $x=17$ ,  $N=3$ ), l/w ratio 4.1–4.5, leaf area 300–1406 mm<sup>2</sup> ( $x=853$ ,  $N=2$ ); lamina apex acute, base cuneate, asymmetrical; margin serrate; teeth simple, spinose, usually irregularly spaced, distant, apex narrowly acute, distal flank straight or convex, proximal flank straight; sinuses angular; venation pinnate; midvein moderately thick; secondary veins festooned semicraspedodromous, seven pairs in portion preserved, with irregular spacing, decurrent attachment, angle of divergence 15–36°, primary course looping to ~½ distance to margin then forking to sub- and superadjacent secondaries, secondary loops with tertiary branches to teeth; tertiary veins reticulate; areoles polygonal; marginal vein present.

**Discussion**—This species, with its sharp, spinose teeth, and a marginal vein (Fig. 10, 1P) resembles some extant species of *Quercus* L. but the presence of festooned semicraspedodromous secondary veins excludes these specimens from that genus (Schorn 1966). These specimens resemble extant *Mahonia lanceolata* (Benth) Fedde (1901) (Güner and Denk 2012) and the fossil species *M. cuprovallis* Axelrod (1966) from the Eocene Copper Basin flora of Nevada (Axelrod 1966), and *M. subdenticulata* (Lesquereux) MacGinitie (1953) from Mormon Creek, Ruby Basin, Beaverhead Basins and Florissant floras (Table 2). For spinose teeth on each margin, *Mahonia cuprovallis* has 11–17, *M. subdenticulata* has 5–9, while our specimens have at least eight. Another

similar example is an unnamed species, “*Mahonia* sp.” found in the Whitecap Knoll flora of the John Day Formation, Oregon, USA at ca. 38.8 Ma (Manchester 2000: Fig. 4F, M).

PROTEALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820  
 PLATANACEAE T. LESTIBOUDOIS, 1826  
 PLATANUS LINNAEUS, 1753  
 PLATANUS CF. EXASPORA MEYER & MANCHESTER, 1997

FIG. 1S

**Referred specimens**—UF 256-21079, 21248a, 21548, 59201, 59202.

**Description**—Lamina widely ovate, symmetrical, unlobed, notophyll, length ~78 mm, width 29–60 mm ( $x=40$ ,  $N=5$ ), l/w ratio 1.3, leaf area estimate 3145 mm<sup>2</sup>, partial petiole length 7.7 mm; lamina apex acute, base cordate; margin serrate; teeth simple to sometimes compound with smaller teeth on proximal flank, falcate, usually regularly spaced and distant, apex acute and glandular, distal flank concave to straight, proximal flank straight to convex; sinus curved to rarely acute; primary venation short suprabasal actinodromous; agrophic veins simple; secondary venation pinnate, craspedodromous, seven pairs, spacing irregular, attachment excurrent or rarely deflected, angle of divergence 30–47°, course straight, rarely dividing to margin; secondary veins entering teeth accompanied by a series of decreasing size loops of higher order veins; tertiary venation alternate percurrent; higher order venation orthogonal; marginal vein present.

**Discussion**—Although unlobed, these specimens are consistent in leaf architecture with extant *Platanus*. Extant *Platanus occidentalis* L. (1753) can have similar leaves with actinodromous primary veins, falcate teeth with glands, rounded sinuses, percurrent tertiaries, orthogonal higher order venation, and a marginal vein. These characters are also found in *P. exaspera* from Bridge Creek and Badger’s Nose floras (Meyer and Manchester 1997, Myers 2006). Although *P. exaspera* typically has prominently trilobed leaves but also have occasional ovate unlobed laminae like the one figured here (Fig. 1S, Newberry 1898, Meyer and Manchester 1997). We have not recovered the more typical, prominently lobed, *P. exaspera* leaves from Teater Road, however, so we are hesitant to place these specimens formally in the same species. Similar unlobed *Platanus* specimens are found in Whitecap Knoll flora (Table 2). Specimen UF 21258 has a marginal vein, and serrate margin with one tooth with a visible gland, but the tertiary and higher order veins are not preserved. Another possible platanoid leaf is UF

21071, with curving secondaries, falcate to rounded teeth and a marginal vein. Silicified wood of Platanaceae is also represented in the nearby Late Eocene sites of Post Hammer and Dietz Hill (Wheeler and Manchester 2021, Wheeler et al. 2023) (Table 3).

*Platanus* consists of 6–10 extant species of trees found primarily in temperate to subtropical riparian habitats of the Northern Hemisphere (Mabberley 1993, Meyer and Manchester 1997, GBIF 2021, PoWO 2023).

PLATANUS SP. ACHENES

FIG. 1M

**Referred specimens**—UF 256-20734a, 20750, 20824a.

**Description**—Isolated achenes; obtriangular in longitudinal outline, length 4–6 mm ( $x=5$ ,  $N=3$ ), width 1–2 mm ( $x=1.5$ ,  $N=3$ ) at widest point, persistent curved style 1.8 mm long, with a ventral slit extending full length of achene; achene subtended by hairs about 3.7–4.4 mm long ( $x=4.1$ ,  $N=3$ ) radiating from the basal portion.

**Discussion**—These achenes are consistent with those of extant *Platanus* (Manchester 1986) in shape and presence of a basal tuft of dispersal hairs (Fig. 1M). Isolated fossil *Platanus* achenes are also found in the Whitecap Knoll and Bridge Creek floras (Table 2).

SAXIFRAGALES BERCHTOLD & J. PRESL, 1820  
 HAMAMELIDACEAE R. BROWN, 1818A  
 CF. PARROTIA C.A. MEYER, 1831

FIG. 3Q

**Referred specimen**—UF 256-21359.

**Description**—Lamina symmetrical, elliptic, unlobed, small, length 24 mm, width 16 mm, l/w ratio 1.5, leaf area estimate 252 mm<sup>2</sup>, petiole length 5 mm; lamina apex and base obtuse, base highly asymmetrical or portion missing; margin serrate; teeth simple, irregularly spaced, distant, apex acute, distal flank concave or straight, proximal flank convex or straight; sinus shallow rounded; venation pinnate; midvein weak; mid to upper secondaries veins craspedodromous, three pairs of secondaries, one pair of weak secondaries near apex, spacing irregular, excurrent attachment, angle of divergence 40–70°, decreasing towards apex, course sinuate to smoothly arching; basal secondary semicraspedodromous, angle of divergence 40°; intersecondaries 0–2 per intercostal, extending ~½ distance to margin and merging with tertiary vein; 1–2 exmedial tertiary branches of distal portion of secondaries terminate in teeth; few mixed percurrent tertiary veins; higher order venation not preserved.

**Discussion**—This specimen is similar to *Parrotia*

*brevipetiolata* Meyer and Manchester (1997), from the Bridge Creek and Badger's Nose floras (Myers 2006), in shape, venation, and teeth, but the diagnostic feature of the short swollen petiole remains unknown for this incomplete specimen. The right portion of the leaf base is difficult to interpret (Fig. 3Q), is it missing, folded or is the lamina naturally highly asymmetrical? If the leaf is naturally highly asymmetrical, then the basal margin is delimited by the lowermost secondary vein, a key character for *Parrotia* (Meyer and Manchester 1997).

*Parrotia* consists of 2–3 extant species of trees, native to the mountains of Transcaucasia, Iran (Mediterranean climate) and China (subtropical climate) (Adroit et al. 2020, GBIF 2021, PoWO 2023).

GROSSULARIACEAE DE CANDOLLE, 1805

*RIBES* LINNAEUS, 1753

*RIBES* SP.

FIG. 2G

**Referred specimens**—UF 256-21241.

**Description**—Lamina very widely ovate, symmetrical, unlobed or possibly shallow tri-lobed, small, length 48 mm, estimated width 50 mm, l/w ratio 1.0, leaf area estimated 1625 mm<sup>2</sup>, petiole missing; lamina apex obtuse; base cordate; margin crenate; teeth simple, usually regularly spaced and close, apices rounded, distal and proximal sides convex; principal vein terminating at tooth apex, looped major accessory veins present; sinuses angular, occasionally with narrow extension 1.0 mm into the lamina; primary venation basal actinodromous, with simple agrophic veins that terminate in rounded teeth; lateral primary angle of divergence 40–55°; secondary venation pinnate, craspedodromous, three pairs, spacing irregular, excurrent attachment, angle of divergence 26–32°, course straight; tertiary venation percurrent; pair of basal tertiary veins extending into cordate lobes; quaternary veins pentagonal; lamina with evenly to randomly spaced glands.

**Discussion**—The margin of this leaf type is only faintly lobed, with prominent crenations (Fig. 2G). We compared this with extant *Ribes sativum* (Reichenbach) Syme (1865), which is similar in characters of shallow lobes, palmate venation, rounded teeth, angular sinuses with narrow extension into the lamina, agrophic veins, and craspedodromous secondaries. The rounded teeth with a median principle vein and looped accessory veins are similar to those of extant *R. amarum* McClatchie (1894) but we were unable to confirm that the tooth apices of the fossil are glandular. The Teater Road specimens are similar to *R. webbia* Wolfe (1964) from

the Miocene Stewart Valley flora of Nevada, in shallow lobing and rounded teeth, but they can differ by having venation that ranges from actinodromous to slightly palinactinodromous (Hermesen 2005). Unlobed *Ribes* leaves also occur in the Bridge Creek flora (Table 2; Meyer and Manchester 1997).

These specimens are also similar to *Fremontodendron lobatum* (Axelrod) Fields (2021) from the Miocene of California; however, in *F. lobatum* the teeth are malvoid; crenations if present are not prominent, and there is no mention of laminar glands (Fields 2021). Specimen UF 256-21095 is a small, presumably juvenile leaf lacking palmate venation but has rounded teeth with evenly spaced glands in the lamina.

*Ribes* consists of 150–192 extant species of low shrubs found primarily in subarctic to temperate regions and tropical mountains (Mabberley 1993, GBIF 2021, PoWO 2023).

MALPIGHIALES JUSS. EX BERCHTOLD & J. PRESL, 1820

MALPIGHIACEAE JUSSIEU, 1789

CF. *HETEROPTERYS* KUNTH, 1822

FIG. 2H

**Referred specimen**—UF 256-20846.

**Description**—Fruit samaroid; curved, with an elongate lateral wing with arching venation resembling that of *Acer*, and two smaller “wings” proximal to the fruit body; fruit length 19 mm, width 8 mm. Major wing ovate, length 15 mm, width 8 mm, one margin convex, thickened, opposite margin sinuate basally, then convex apically; wing apex rounded; venation with numerous parallel major and minor veins, bifurcating 1–2 times, anastomosing and curving to one of the lateral margins; axis of nut at 20° degree angle to wing; two smaller wings, presumably perianth-derived, originate from apical portion of nutlet; these secondary wings possibly oval, length 4.2 mm, width 1.4 mm, distal margin straight, proximal margin convex, apex acute; nutlet oval, length 3.0 mm, width 2.0 mm, reticulate, nutlet angle 60°; apex obtuse; attachment scar on distal side of nutlet; attachment angle 35°.

**Discussion**—Although this samara superficially resembles *Acer*, it is distinguished by the smaller wings or appendages arising from the fruit body. Samaras with a nutlet subtending one major wing and two smaller wings are found in *Luetzelburgia* Harms (1922) and *Vataireopsis* Ducke (1932) (Fabaceae), but they lack an attachment scar on the distal side of the nutlet, and the fruits are nearly five times larger than this specimen (de Lima 1980, Kirkbride et al. 2003, Cardoso et al. 2014). *Acer*-like

samaras also occur in some genera of Malpighiaceae such as *Banisteriopsis* C.B. Rob. (1910) and *Heteropterys* Kunth (1822) (van Roosmalen 1985). In both genera, wing striation, thickened proximal margin, persistent structures (i.e., perianth, filaments) and or lobing from the base of the fruit body, and wing and fruit body size are similar to our specimen.

*Heteropterys* consists of 164 accepted species of lianas, shrubs or trees found in Tropical and Subtropical America, and west Tropical Africa (van Roosmalen 1985, PoWO 2024). *Banisteriopsis*, which also has similar samaras, consists of 62 accepted species of shrubs or lianas found from Mexico to Tropical America (van Roosmalen 1985, PoWO 2024).

SALICACEAE MIRBEL, 1815  
MORPHOTYPE TRL 04

FIG. 3R, W

**Referred Specimens**—UF 256-21254a, 34091.

**Description**—Lamina elliptic, unlobed, length 55 mm, width 24–33 mm ( $x=29$ ,  $N=2$ ), l/w ratio 2.3, leaf area 984–1874 mm<sup>2</sup> ( $x=1429$ ,  $N=2$ ), petiole length 13.5 mm; lamina apex acute, base obtuse and asymmetrical; margin serrate; one order of teeth, angled close to margin, regularly spaced, close, apices rounded and glandular, distal flank straight, proximal flank basally straight then highly convex; sinuses rounded or angular; venation pinnate; midvein moderately thick, sinuous; secondary venation semicraspedodromous, at least six pairs, spacing irregular, excurrent attachment, angle of divergence 35–60°, course curved and sinuous, with exmedial looping near margin; exmedial branching of tertiary veins entering teeth from exmedial secondary looping; a few percurrent and epimedial tertiary veins preserved; higher order veins not preserved.

**Discussion**—Leaves with this suite of morphological characters can be found in *Salix* L. (1753) and *Populus* L. (1753). These specimens conform to *Salix*, Group 1 of Buechler (2014), characterized by brochidodromous secondary veins with two series of loops (Fig. 3R), exmedial branching of tertiary veins entering teeth from exmedial looping of secondary veins, and glandular teeth (Fig. 3W). Some fossils of this kind have been treated as *Salix hesperia* (Knowlton) Condit (1956) (Becker 1973). These fossils also resemble *Populus payettensis* (Knowlton) Axelrod (1944) in overall shape, slightly asymmetrical base, sinuous midvein, angle of secondaries, margin, venation, and long petiole (Knowlton 1898, Axelrod 1944). *Populus payettensis* specimens are found in York Ranch and Beaverhead Basins floras, while *S. hesperia* is found

in the Metzler Ranch and York Ranch floras (Table 2). We have not found any fruits or seeds of *Populus* or *Salix* in the Teater Road shales.

FABALES BROMHEAD, 1838

FABACEAE LINDLEY, 1836

CERCIS LINNAEUS, 1753

CERCIS HERBMEYERI JIA & MANCHESTER, 2014

FIG. 2L

*Cercis herbmeyeri* Jia and Manchester, 2014, Int. J. Plant Sci. 175, p. 606, fig. 4.

**Holotype**—Designated by Jia and Manchester 2014: UF 256-20675.

**Paratypes**—UF 256-20678, 20679, 20682, 20683, 20685, 20686, 20687, 20689, 20690, 20691, 20693, 20694.

**Additional referred specimens**—UF 256-20676a, 20680a, 20681, 20684, 20688, 20696, 20698, 76264.

**Description**—Fruit, as described by Jia and Manchester (2014).

**Discussion**—Here we illustrate another pod of *Cercis herbmeyeri* (Fig. 2L), supplemental to those already figured by Jia and Manchester (2014). Fruits of *C. maurerae* Meyer and Manchester (1997) from the Bridge Creek flora are similar but tend to be larger (Table 2).

*Cercis* consists of 6–10 species of trees, found in mesic to xeric habitats of temperate to subtropical regions, Northern Hemisphere (Fritsch et al. 2018, GBIF 2021, PoWO 2023).

CERCIS PARVIFOLIA LESQUEREUX EMEND. JIA & MANCHESTER, 2014

FIG. 2M

*Cercis parvifolia* Lesquereux emend. Jia and Manchester, 2014, Int. J. Plant Sci. 175, p. 603, figs. 2, 3.

**Referred specimens**—UF 256-21153–21156, 21161, 21162, 21164, 21653, 34111, 53983.

**Description**—Leaf, as described by Jia and Manchester (2014).

**Discussion**—Here we reillustrate a relatively complete specimen of *Cercis parvifolia* (UF 256-21164), with a broadly rounded base, entire margin, three actinodromous primary veins, and agrophic veins (Fig. 2M) (see Jia and Manchester 2014). *Cercis parvifolia* specimens are also found in Metzler Ranch and Beaverhead Basins floras, as well as the type locality, Florissant flora (Table 2). Jia and Manchester (2014) suggested that the relatively small leaf size of *C. parvifolia* may indicate an adaptation for dry conditions, but the leaves from Teater Road tend to be larger than those from Florissant.

CF. GYMNOCLADUS LAMARCK, 1785

CF. GYMNOCLADUS DAYANA (KNOWLTON) CHANEY & AXEL-  
ROD, 1959

FIG. 2N

cf. *Gymnocladus dayana* (Knowlton) Chaney and Axelrod, 1959, Carnegie Inst. Wash. Publ. 617, pgs. 187–188, pl. 37, figs. 7–9.cf. *Salix dayana* Knowlton, 1902, U.S. Geol. Surv. Bull. 204, p. 31, pl. 2, fig. 10 only.**Referred specimen**—UF 256-21073.**Description**—Leaflet elliptic, symmetrical, unlobed, small, length 44 mm, width 28 mm, l/w ratio estimate 1.6, leaflet area estimate 928 mm<sup>2</sup>, pulvinus with transverse striations, 8 mm long, 1.8 mm wide; lamina apex missing; base rounded and slightly cordate; margin entire; venation pinnate; midvein moderately thick, straight; secondary venation brochidodromous, at least six pairs, spacing irregular, excurrent attachment, angle of divergence 60–90°, course smoothly curved upwards, sometimes sinuate; epimedial tertiaries reticulate, proximal course acute or obtuse to midvein; tertiary and quaternary veins reticulate.**Discussion**—The leaflet morphology of this and the following species are consistent with extant Fabaceae. This specimen resembles the fossil species *Gymnocladus dayana* (Fig. 2N) (Chaney and Axelrod 1959, see pl. 37, fig. 8), although the specimens illustrated by Knowlton (1902) do not have a cordate base. As mentioned in Chaney and Axelrod (1959), *G. dayana* bears a close similarity to extant *G. dioicus* (L.) Koch (1869), although *G. dioicus* does not have a slightly cordate leaf base. At present, *Gymnocladus* leaflets have only been found in Teater Road and Green River floras (Table 2).*Gymnocladus* consists of 5–6 extant species of trees found in eastern North America, eastern Himalayas to south China and Indo-China (Mabberley 1993, GBIF 2021, PoWO 2023).

CF. GYMNOCLADUS HESPERIA (BROWN) MACGINITIE, 1969

FIG. 2K

*Gymnocladus hesperia* (Brown) MacGinitie, 1969, Univ. Calif. Publ. Geol. Sci. 83, p. 109, pl. 13, figs. 1, 3, 6.*Cassia hesperia* Brown, 1934, U.S. Geol. Surv. Prof. Pap. 185-C, p. 58, pl. 12, figs. 1, 4.**Referred specimen**—UF 256-21082.**Description**—Leaflet ovate, symmetrical, unlobed, small, length 54 mm, width 27 mm, l/w ratio 2, leaflet area estimate 964 mm<sup>2</sup>; lamina apex acuminate; base cuneate; margin entire, petiolule 5 mm long, 1.7 mm

wide, pulvinus transversely striated; venation pinnate; midvein stout, straight; higher order venation weak; secondary venation brochidodromous, ~six pairs, spacing irregular, excurrent attachment, angle of divergence 45–70°, increasing apically, course relatively straight basally, smoothly arched apically; tertiary veins mixed percurrent/reticulate; epimedial tertiaries mixed percurrent, proximal course perpendicular to midvein, distal course basiflex; quaternary veins reticulate; 0–1 intersecondaries per intercostal area, extending to ~½ distance to margin, basiflex.

**Discussion**—For an example of extant species with leaflets similar to this specimen, we selected *Wisteria sinensis* (Sims) de Candolle (1825). In *W. sinensis* the secondaries can sometimes bifurcate near the margin and intersecondaries are 1–2 per intercosta. This fossil is also similar to extinct *Gymnocladus hesperia* of the Green River flora (see pl. 12, fig. 4 in Brown 1934, and pl. 13, fig. 3 in MacGinitie 1969) (Table 2). According to MacGinitie (1969), *G. hesperia* is similar to extant *G. dioicus*, although in *G. dioicus*, there are 1 or 2 intersecondaries per intercostal area.

CF. ACROCARPUS R. WIGHT EX ARNOTT, 1838

FIG. 2Q

**Referred specimens**—UF 256-20674, 34079a.**Description**—Fruit a legume, linear, elongate, length 40 to > 77 mm, width 9–14 mm (x=11, N=2); apex acute; base tending elongate, sides straight; placental suture winged, width 3–4 mm; non-placental suture winged, width 2 mm; seed outline transverse to the fruit length; length 8.3 mm, width 7.0 mm.**Discussion**—Oblong or linear fruits with relatively narrow wings along both sutures (Fig. 2Q) occur in various extant genera of Fabaceae including *Acrocarpus*, *Pericopsis* Thwaites (1864), and *Aganope* Miquel (1855) (syn. *Xeroderris* Roberty (1954), *Ostryoderris* Dunn (1911)). *Acrocarpus* is dehiscent while *Pericopsis*, *Xeroderris*, and *Aganope* are indehiscent (Gunn 1991, Herendeen 1992, Kirkbride et al. 2003). The Teater Road fossils are similar to those that were referred to cf. *Acrocarpus* from the Eocene Claiborne Formation of Mississippi in the eastern USA (Herendeen 1992, Blanchard et al. 2016).*Acrocarpus* consists of 1–2 species of large trees found in the Indo-malaysian region, in tropical forest with wet and fertile soil (Mabberley 1993, Hou 1994, Blanchard et al. 2016, GBIF 2021, PoWO 2023).MILLETTIEAE M<sub>1</sub>Q, 1855/CAESALPINIEAE R<sub>1</sub>CHB., 1832  
MORPHOTYPE TRR 01

FIG. 2P, V

**Referred specimens**—UF 256-20695a, b.

**Description**—Fruit a legume, straight, length >32 mm, width 12–15 mm ( $x=14$ ,  $N=2$ ); apex rounded and beaked; base tapered; margins constricted or not constricted; sutures winged along both margins; width of wings 1–3 mm.

**Discussion**—These specimens resemble the pods of extant *Derris* J. de Loureiro (1790), 15–45 spp.), and of *Peltophorum pterocarpum* (de Candolle) Backer ex. K. Heyne (1927) in fruit size, shape, noticeable constrictions, and winged margins (Fig. 2P, 2V) (Kirkbride et al. 2003). These characters are also shared with extinct fruit Morphotype 3 of Herrera et al. (2019) from the Middle to Late Paleocene of Colombia.

GEN. ET SP. INDET.  
MORPHOTYPE TRL 05

FIG. 2S

**Referred specimens**—UF 256-21441, 21635.

**Description**—Leaflet elliptic, symmetrical, unlobed, small, length 21–24 mm ( $x=22$ ,  $N=2$ ), width 10–11 mm ( $x=10.5$ ,  $N=2$ ), l/w ratio 2.0–2.1, leaflet area estimate 143–173 mm<sup>2</sup> ( $x=158$ ,  $N=2$ ), petiole length 2.5 mm, pulvinus transversely striated; lamina apex obtuse; base acute; margin entire; venation pinnate; primary vein weak, straight; secondary venation brochidodromous, seven pairs, irregularly spaced, excurrent attachment, angle of divergence 40–50°, course smoothly curved or sinuate; 0–1 intersecondaries per intercostal, extending to tertiary or outer loop of secondary vein; tertiary venation reticulate; higher order venation not preserved.

**Discussion**—These specimens appear to have a covering of trichomes which obscures the preservation of tertiary and higher order veins (Fig. 2S).

MORPHOTYPE TRR 02

FIG. 2U

**Referred specimens**—UF 256-34104, 34105.

**Description**—Fruit a legume, obovate or elliptic, straight, length 16–30 mm, width 7–8 mm; apex truncate; base tapered; sutures along both margins.

**Discussion**—For an example of an extant genus similar to our specimens, we refer to *Behaimia* Grisebach (1866) (Fabaceae: Millettieae) (Kirkbride et al. 2003), however, the detail of seed orientation is not clear in this fossil. This fruit type (Fig. 2U) appears to be unique to the Teater Road flora.

MORPHOTYPE TRR 03

FIG. 2R

**Referred specimen**—UF 256-20681.

**Description**—Fruit incomplete; linear and slightly curved, length >90 mm, width 14 mm; one end acute, opposite end missing; suture along one side.

**Discussion**—This fruit (Fig. 2R) resembles those of Fabaceae, but preservation is too poor for precise determination.

MORPHOTYPE TRL 06

FIG. 2O

**Referred specimens**—UF 256-21546a, 62699.

**Description**—Leaflet lanceolate, asymmetrical, curved, unlobed, mesophyllous, length 26–47 mm ( $x=36$ ,  $N=2$ ), width 11–17 mm ( $x=14$ ,  $N=2$ ), l/w ratio 2.3–2.7, leaflet area estimate 199–546 mm<sup>2</sup> ( $x=372$ ,  $N=2$ ), petiolule missing; lamina apex acute; base obtuse; margin entire; venation pinnate; midvein moderately thick, curved; secondary venation brochidodromous, ten pairs, irregular spacing, excurrent attachment, secondary course of short loops on one side of midvein, angle of divergence 65–85°, longer loops on other side of midvein, angle of attachment 45–50°; tertiary venation reticulate; 1–2 intersecondaries per intercostal; higher order venation not preserved.

**Discussion**—These specimens resemble the unidentified lanceolate leaflets of Fabaceae in the Eocene of southeastern North America (Herendeen 1992: fig. 247) but secondary looping is nearly symmetrical on both sides of the midvein (Fig. 2O). This species is also similar to *Parvileguminophyllum coloradensis* (Knowlton) Call and Dilcher (1994) from the Green River flora (Table 2, MacGinitie 1969: pl. 14, fig. 8; Call and Dilcher 1994) but is distinguished by a greater number of secondary veins. The Teater Road specimens are also superficially similar to *Quercus* but this morphotype lacks a marginal vein and the lamina is asymmetrical.

MORPHOTYPE TRL 07

FIG. 2T

**Referred specimens**—UF 256-20804, 78822.

**Description**—Leaflet elliptic, unlobed, length > 21 mm, width 2–9 mm, leaflet area estimate 19–123 mm<sup>2</sup> ( $x=71$ ,  $N=2$ ), petiolule length 0.1 mm; lamina apex acute; base obtuse and asymmetrical; margin entire; venation pinnate; midvein distinct; secondary venation poorly preserved except for one basal, camptodromous secondary

vein; higher order venation not preserved.

**Discussion**—The presence of an asymmetrical base with at least one strong camptodromous vein on one side of midvein at the base, a minute petiolule, small lamina size and entire margin (Fig. 2T) suggest a leaflet of Fabaceae. These specimens are similar to *Gleditsia lot-tii* Axelrod (1998) from the Oligocene of eastern Idaho (Axelrod 1998) but preservation of higher order venation is insufficient in these specimens for confirmation. Similar shaped leaflets of *Mimosites acaciaefolius* Berry (1916) occur in the Beaverhead Basins flora (Table 2). Specimen UF 256-20904 may also be Fabaceae judging from the size, shape, and strong asymmetry (midvein close to one margin) and brochidodromous secondary venation. Such characteristics can be found in *Leucaena leucocephala* (Lamarck) de Wit (1961), although the latter has much smaller leaflets.

ROSALES BERCHTOLD & J. PRESL, 1820  
RHAMNACEAE JUSSIEU, 1789  
*PALIURUS* MILLER, 1754  
*PALIURUS FAVONII* UNGER, 1847

FIG. 2W, X

*Paliurus favonii* Unger, 1847, *Chloris* Protogaea, VIII–X, p. 147, pl. 50, fig. 6.

**Referred specimens**—UF256-20906, 21060, 21573, 34103, 87110.

**Description**—Fruit with a central endocarp surrounded by a circular wing 13–22 mm in diameter; receptacle with pronounced rim, receptacle diameter 5 mm; endocarp with ca. ten regularly spaced longitudinal ribs extending from pedicel to receptacle edge, endocarp, two-loculed, 2–3 mm in diameter ( $x=3$ ,  $N=3$ ); wing with entire margin, wavy to clefted in one portion, with radiating venation.

**Discussion**—These specimens (Fig. 2W), some of which were illustrated previously (Burge and Manchester 2008), conform to the fossil species *Paliurus favonii* which was common in the Oligocene to Miocene of Europe and North America. *Paliurus*, confirmed by fruits, is known in the Late Eocene of western North America and Japan, the Miocene of middle latitudes in the Northern Hemisphere, plus the Pliocene and Pleistocene of Japan (Burge and Manchester 2008). Leaves described as *P. florissantii* Lesquereux (1878) are found in the Metzler Ranch and Ruby Basin floras, while other *Paliurus* species occur at Beaverhead Basins and Bridge Creek floras (Table 2). Although fruits are diagnostic for the genus, it can be difficult to distinguish the leaves of *Paliurus* from those of the related genus *Ziziphus* Miller

(1754). A species identified as cf. *Ziziphus* was observed at Whitecap Knoll (Table 2).

*Paliurus* consists of 5–8 species of shrubs or trees found in warm and dry regions of North Africa, southern Europe, Central and South China, Temperate eastern Asia, and Japan (Mabberley 1993, Meyer and Manchester 1997, PoWO 2023).

ROSACEAE JUSSIEU, 1789  
*AMELANCHIER* MEDIKUS, 1789  
*AMELANCHIER* SP.

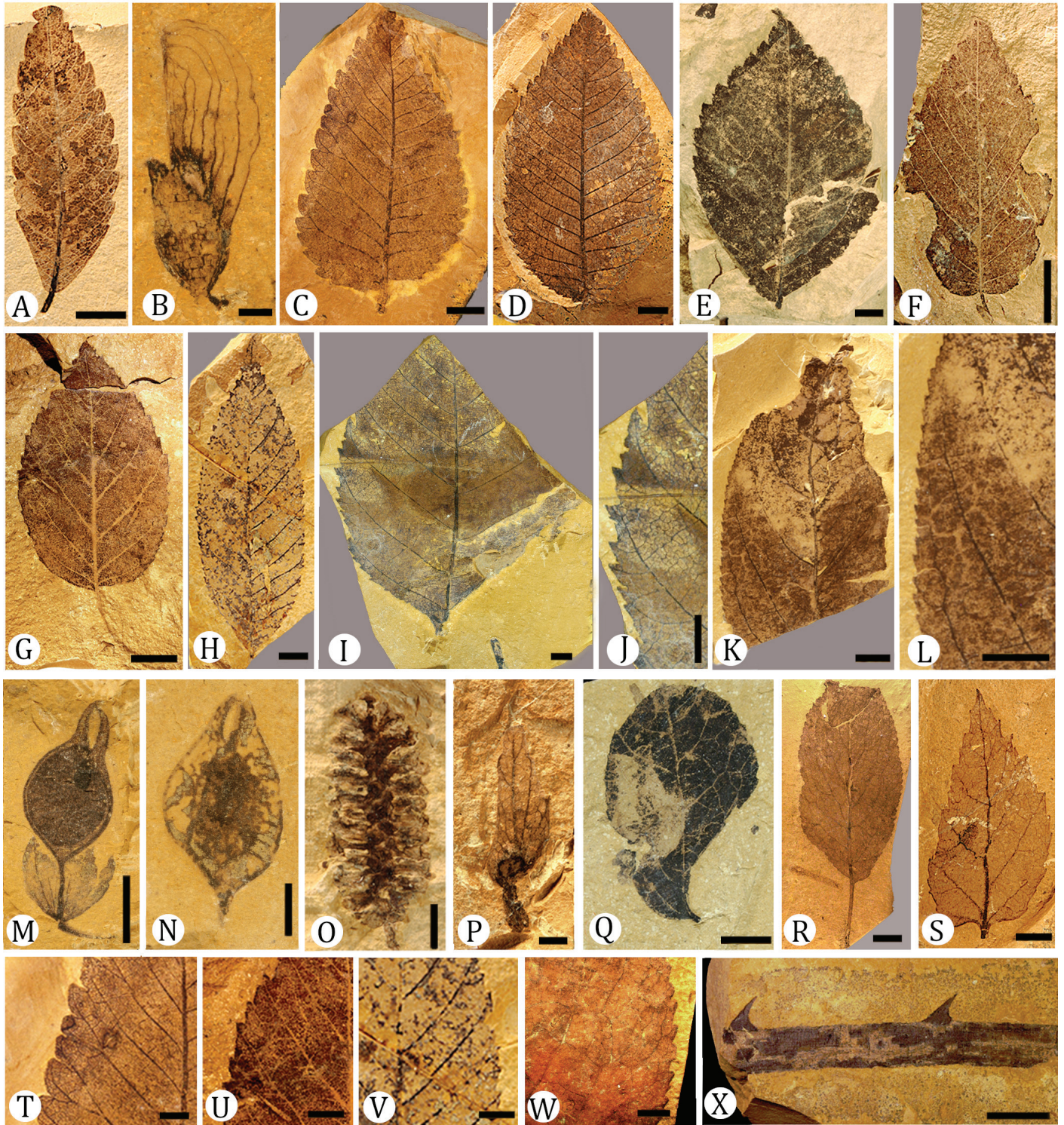
FIG. 3K, L

**Referred specimens**—UF 256-21067, 21255, 21598, 84736.

**Description**—Lamina elliptic or ovate, symmetrical, unlobed, small, length 48–55 mm ( $x=52$ ,  $N=3$ ), width 25–27 mm ( $x=26$ ,  $N=3$ ), l/w ratio 1.7–2.2, leaf area estimate 871–935 mm<sup>2</sup> ( $x=909$ ,  $N=3$ ), petiole missing; lamina apex acute; base rounded, sometimes cordate; margin serrate; teeth simple, usually regularly spaced, distant, slightly falcate, distal flank concave, proximal flank basally straight then convex; sinuses angular or rounded; venation pinnate; midvein weak, sinuous; secondary venation semicraspedodromous, ~ seven pairs, spacing irregular, excurrent attachment, angle of divergence 40°, course of long loops; secondary veins with one series of tertiary exmedial loops which enter the teeth; 1–2 intersecondaries per intercosta, relatively parallel to secondaries, extending up to ½ distance to margin before merging into tertiary veins; tertiary veins percurrent or sometimes reticulate; proximal course of epimedial tertiaries acute to midvein, distal course basiflex to subadjacent secondary; quaternary veins polygonal reticulate.

**Discussion**—For an example of an extant species similar to our specimens, we examined *Amelanchier laevis* Wiegand (1912), which is similar in leaf shape, serrate margin with falcate teeth, semicraspedodromous secondary veins, mixed percurrent tertiaries, and epimedial tertiaries that curve down to subadjacent secondaries (Fig. 3K); however, intersecondary veins are lacking and the teeth are callus tipped in *A. laevis* (Jones 1946). The Teater Road specimens also resemble the fossil species *Amelanchier covea* (Chaney) Chaney and Axelrod (1959) from the Beaverhead Basins and Bridge Creek floras (Table 2), but *A. covea* is widely elliptic and has at least 14 secondary vein pairs.

*Amelanchier* consists of 24–33 extant species of shrubs and trees, found in forest and dry areas of North America, Europe, Mediterranean, Caucasus, Central and Eastern



**Figure 3.** A. *Cedrelospermum* sp., leaf, UF256-21107. B. *Cedrelospermum lineatum* (Lesquereux) Manchester, fruit, UF256-20914. C. *Ulmus chuchuanus* (Berry) LaMotte, UF256-21320. D. *Ulmus chuchuanus*, UF 256-21282. E. *Ulmus okanaganensis* Denk and Dillhoff leaf, UF256-21276. F. *Alnus newberryi* Meyer and Manchester, UF 256-21368. G. *Alnus newberryi*, UF 256-34074. H. Morphotype TRL 08, *Carpinus*-like leaf, UF 256-21272. I, J. Morphotype TRL 09, *Corylus* like leaf, UF256-21244. K, L. *Amelanchier* sp., finely serrate leaf, UF 256-21598. M. *Ulmus okanaganensis* Denk and Dillhoff, stipitate fruit with intact perianth, very narrow wing, and two persistent styles, UF 256-20910. N. *Ulmus* sp. 1, winged fruit with fimbrial vein and apical stigmatic notch, UF 256-20907. O. *Alnus* sp. 1, infructescence, UF 256-20915. P. *Carpinus* sp., fruit, UF 256-21037. Q. cf. *Parrotia*, UF 256-21359. R. Morphotype TRL 04, with similarity to *Salix*, UF 256-34091. S. cf. *Crataegus*, UF 256-78823. T. Detail from C. U. Detail from G. V. Detail from H. W. Detail from R. X. Morphotype TRB 01, twig with prickles, UF 256-34078. Scale bars: A, C–E, H–L, Q, R, U=5 mm; B=1 mm; F, G, X=10 mm; M, N, P, T, V, W=2 mm; O, S=3 mm.

China to Japan (Mabberley 1993, GBIF 2021, PoWO 2023).

CF. *CRATAEGUS* TOURN. EX. LINNAEUS, 1753

FIG. 3S

**Referred specimen**—UF 256-78823.

**Description**—Lamina ovate, symmetrical, unlobed, nanophyll, length 20 mm, width 10 mm, l/w ratio 1.9, leaf area estimate 138 mm<sup>2</sup>, petiole fragmented, 3 mm long; lamina apex acute, base cordate; margin serrate; teeth compound, two orders of teeth, one minor tooth between secondaries, regularly to irregularly spaced, distant, apex minutely glandular, distal and proximal flanks straight, proximal longer than distal; sinuses angular; venation pinnate; midvein sinuate; secondary venation craspedodromous, five pairs, spacing irregular, angle of divergence 23–61°, sinuate, arching to straight; basal pair of secondaries semicraspedodromous; secondaries with exmedial branching of minor secondaries to teeth; tertiaries reticulate; higher order veins not preserved.

**Discussion**—Ovate, unlobed leaves with compound serrate margins, glandular teeth, and craspedodromous secondary venation (Fig. 3S) occur in Rosaceae, as in the genera *Crataegus*, *Malus* Miller (1754) and *Sorbus* L. (1753). *Malus* leaves have a cordate base, and sometimes have deeply lobed margins. In the case of *Sorbus*, one would need a complete leaflet to check for the presence of gland clusters at the point of attachment to the rachis (Sargent 1933, Robertson et al. 1992). Such clusters are not evident in our specimen. To confirm the identification of *Crataegus*, one would need more fossil specimens to document the variation in leaf morphology such as the degree of leaf incision and the presence or absence of intersecondary venation (Meyer and Manchester 1997). We tentatively place this specimen as cf. *Crataegus* as there is only one specimen. This specimen shows some similarity to the leaves treated as *Alnus newberryi* Meyer and Manchester (1997) in this paper; however, in cf. *Crataegus* the secondary vein course is sinuate, the secondary vein spacing is irregular and tertiary veins are reticulate, rather than percurrent. Also, *Crataegus* has fairly expanded glands while *Alnus* has narrowly glandular teeth. This taxon has not been noticed among our other selected sites of western United States (Table 2).

*Crataegus* consists of 200–300 species of shrubs or trees, found in temperate Northern Hemisphere to Central America (Mabberley 1993, Meyer and Manchester 1997, GBIF 2021, PoWO 2023).

ROSACEOUS PRICKLY TWIG

FIG. 3X

**Referred specimens**—UF 256-31408, 31409, 34078.

**Description**—Twig with alternate, broad based perpendicular prickles; prickle length 1.5–6.0 mm, width 1.1–4.6 mm. One side straight, other side straight to convex.

**Discussion**—The sharp projections on these twigs represent prickles of the kind found in the rosaceous genera *Rosa* L. and *Rubus* L. Our specimens resemble those attributed to *Rosa hilliae* Lesquereux (1883) (Becker 1969, see pl. 31, figs. 2, 3) from the Metzel Ranch, Ruby Basin, York Ranch, Beaverhead Basins, and possibly Whitecap Knoll floras (Table 2). The position of the prickles in our specimens (Fig. 3X) are different from what one finds in *Paliurus* where the spines (modified stipules) are paired at the nodes (Shahbaz and Shareef 2018, UF 256-0987). *Rosa hilliae* was diagnosed based on leaves, so due to the absence of leaves, these specimens are assigned simply to Rosaceae sp.

ULMACEAE MIRBEL, 1815

*CEDRELOSPERMUM* SAPORTA EMEND. MANCHESTER, 1987A  
*CEDRELOSPERMUM LINEATUM* (LESQUEREUX) MANCHESTER, 1987A

FIG. 3B

*Cedrelospermum lineatum* (Lesquereux) Manchester, 1987a, Rev. Palaeobot. Palynol. 52, p. 124, pl. I, figs. 5–9, pl. II, figs. 1–3, 5, 8–10.

*Banksites lineatus* Lesquereux, 1883, Rep. U.S. Geol. Survey Terr. 8, p. 165, pl. 32, fig. 21.

**Referred specimens**—UF 256-5475, 5476, 20912, 20913, 20914.

**Description**—Fruit samaroid, consisting of an oval or ovate endocarp at basal end, with two unequal size wings; fruit length 8–16 mm ( $x=11$ ,  $N=3$ ), width 3–4 mm ( $x=3.5$ ,  $N=3$ ); fruit apex obtuse; base acute or obtuse; endocarp length 4–6 mm ( $x=4.6$ ,  $N=4$ ), width 2–4 mm ( $x=2.5$ ,  $N=4$ ); primary wing length 6–11 mm ( $x=9$ ,  $N=3$ ), width 3–4 mm ( $x=3.6$ ,  $N=3$ ), with straight lateral margins and rounded apex, with marginal vein around entire wing, with 6–7 well defined bifurcating veins that converge at stigmatic area located at distal end along flank facing secondary wing; secondary wing minute, thick, triangular, aligned with the long axis of the endocarp, ca. 0.8 mm long; pedicel 0.75 mm long.

**Discussion**—Samaras from Teater Road were included in an earlier article indicating ulmaceous affinity for the extinct genus *Cedrelospermum* (Pl. 2, fig. 8, 10 in Manchester 1987a). The ulmaceous affinity is supported by the bicarpellate configuration inferred from the two

wings, the oval endocarp, together with converging veins at the distal stigmatic area of the wing, and a marginal vein surrounding the wing (Fig. 3B) and is supported also by the vegetative features of leaves and phylotaxy observed in fossil twigs bearing these fruits from the Green River and Florissant floras, and by the pollen retrieved from staminate flowers (Manchester 1989a). This extinct genus is also known from the Cenozoic of Europe and Asia (Wilde and Manchester 2003, Jia et al. 2019). The configuration of the two unequal wings, and fruit and endocarp size, relate these fruits to the species *Cedrelospermum lineatum*, which was previously noted from Florissant, Clarno Formation, and Bridge Creek floras (Table 2, Manchester 2001).

*CEDRELOSPERMUM* SP.

FIG. 3A

**Referred specimens**—UF 256-20703b, 20935, 21103, 21104a, 21107, 21114, 21115a, 21119a, 21121, 21296, 21351, 21546b, 21595, 21616, 21625, 34080, 34115, 34116, 59262, 87134, 259-10884.

**Description**—Lamina elliptic or seldom ovate, unlobed, nanophyll or small, symmetrical or asymmetrical, length 11–42 (49) mm ( $x=22$ ,  $N=35$ ), width 4–14 (22) mm ( $x=9$ ,  $N=37$ ), l/w ratio 2–6, leaf area estimate 33–322 mm<sup>2</sup> ( $x=140$ ,  $N=34$ ), petiole short, thick, up to 4.2 mm long; lamina apex acute or acuminate; base rounded, asymmetrical or symmetrical, or base cuneate, angle acute and symmetrical; margin serrate; teeth simple, rounded to widely triangular, regularly spaced, distant, apex acute or rounded, distal flank flexuous, sometimes straight or concave, proximal flank flexuous, convex, or sometimes straight, tooth tip apiculate or attenuate; sinuses angular; venation pinnate; midvein stout; secondary venation craspedodromous, 8–12 pairs, spacing irregular, excurrent attachment, angle of divergence decreasing from base to apex, basal 43–78°, middle 35–70°, apical 25–49°, course straight to smooth curving; secondary simple to branched 1–2 per side; exmedial branches of minor secondaries or tertiaries mostly to sinus; less than one intersecondary per intercostal, parallel to secondaries, bifurcate < to > ½ distance to margin; tertiary venation mostly alternate percurrent; quaternary venation mostly alternate percurrent; free ending fifth order veins.

**Discussion**—These specimens do show a range of variation in terms of width. These specimens conform to extant Ulmaceae in characters of elliptic and often asymmetrical leaves, with blunt non-glandular teeth that are enervated submedially, and short thick petiole

(Manchester 1989b), as seen for example in *Hemiptelea* Planchon (1872), *Planera* J.F. Gmelin (1791), *Ulmus* L. (1753) and *Zelkova* Spach (1841). The presence of one tooth per secondary vein is characteristic for *Cedrelospermum*, and is also typical for *Hemiptelea*, *Zelkova* and some species of *Ulmus*, but *Cedrelospermum* leaves tend to be narrower, i.e., have a higher length/width ratio. The Teater Road leaves, with prominent, rounded to triangular teeth, secondaries with exmedial branching to sinuses and teeth, intersecondaries present, alternate percurrent tertiaries (some leaves are reticulate), and free ending ultimate veins (Fig. 3A) match the extinct *Cedrelospermum*, particularly *C. nervosum* (Newberry) Manchester (1989b) from the Middle Eocene of Oregon and Wyoming (Manchester 1989b). Our leaves fit the size range for those on reproductive branches of *C. nervosum* known from the Green River flora (Manchester 1989b). The leaves differ from *C. nervosum*, however, because the secondaries are not all curved, and intersecondaries extend farther toward the leaf margin. *Cedrelospermum nervosum* specimens are also found in the Green River, Mormon Creek and York Ranch floras (Table 2), although the specimens from York Ranch need to be reinvestigated. Some leaves of this genus were previously identified as *Zelkova drymeja* (Lesquereux) Brown (1946) (Becker, 1961, 1966, 1969, 1972). A possible fragment of *Cedrelospermum* (UF 256-21104b) is attached to the stem associated with 21104a. Specimen UF 256-21616 is larger than average for *Cedrelospermum* sp. at Teater Road.

*ULMUS* LINNAEUS, 1753

*ULMUS CHUCHUANUS* (BERRY) LAMOTTE, 1952

FIG. 3C, D, T

*Ulmus chuchuanus* (Berry) LaMotte, 1952, Geol. Soc. Am. Mem. 51, p. 347.

*Ulmus columbianus* Berry (non Penhallow), 1926, Canada Geol. Surv. Bull. 42, p. 108, pl. 15, fig. 7.

**Referred specimens**—UF 256-21063, 21075, 21086, 21116, 21152a, 21252, 21253a, 21263–21271, 21273, 21275, 21277–21280, 21282, 21285, 21286, 21289, 21291, 21293, 21297, 21300, 21304–21306, 21309, 21310, 21312, 21314a, 21315, 21317, 21318, 21320–21324, 21325a, 21326, 21328–21330, 21331a, 21332, 21333, 21335, 21336, 21339a, 21340, 21342–21345, 21349, 21350, 21353, 21354–21358, 21360–21365, 21478b, 21537a, 21557, 21558, 21560, 21561, 21634, 21646, 31405b, 34072, 59161, 59172–59175, 59177, 59178, 59179a, 59180–59182, 59187, 59188, 59192, 59199, 59200, 59203, 59222, 59284, 59293, 59370b, 62696, 78155, 78827, 78828, 79035, 84744, 87115.

**Description**—Lamina widely or narrowly ovate, rarely elliptic, unlobed, asymmetrical to rarely symmetrical, nanophyll or small, length 8–65 mm ( $x=39$ ,  $N=72$ ), width 5–46 mm ( $x=21$ ,  $N=109$ ), l/w ratio 0.9–2.7, leaf area estimate 27–1655 mm<sup>2</sup> ( $x=606$ ,  $N=69$ ), petiole length 1–7 mm; lamina apex acute, base rounded or slightly cordate, highly asymmetrical to symmetrical; margin simple or compound serrate with two orders of teeth, smaller tooth on proximal flank of primary tooth; teeth rounded to widely triangular, regularly spaced, close or distant, apex sometimes apiculate but non-glandular; distal flank straight, concave to rarely sinuous, proximal flank convex to sinuous; sinuses angular; venation pinnate; midvein weak or moderate, straight; secondary venation craspedodromous, 12–18 pairs, irregular spacing, excurrent attachment, angle of divergence decreasing from base to apex, basal 60–110°, middle to apical 52–74°, course straight to slightly curved, rarely simple to frequently branched at 4–9 per side, rarely less than  $\frac{1}{2}$  to more frequently  $\frac{3}{4}$  distance to margin, exmedial branches of secondaries 1–3, with tertiaries to teeth and sinus; intersecondaries less than one per intercoastal, extend  $\leq 1/2$  distance to margin, bifurcates at end or loops to subadjacent secondary; tertiary venation perpendicular to secondaries, mostly alternate percurrent, sometimes reticulate; quaternary venation reticulate; areoles polygonal.

**Discussion**—These leaves are similar to *Ulmus*, *Zelkova*, and *Planera* (Ulmaceae). *Zelkova*, however, usually has exclusively simple teeth. Compared to *Ulmus*, *Planera* often has more intersecondary veins, and in *Zelkova*, dichotomies of the secondary veins near the margin occur less than four times per leaf (Burnham 1986) and tertiaries are mostly conspicuously branched (Tanai and Wolfe 1977). *Ulmus chuchuanus* differs from *U. okanaganensis* Denk and Dillhoff (2005) in that *U. chuchuanus* has an ovate shape, rounded leaf base, basal secondary angle of attachment 60–110°, and higher number of secondary vein pairs. Our leaves are similar to *U. chuchuanus* from the early middle Eocene of British Columbia and Washington, in shape, short petiole, base shape, higher number of secondary vein pairs, and tooth shape (Fig. 3EC, 3D) (Denk and Dillhoff 2005), but the Teater Road specimens differ in the number of exmedial branching secondary veins. This species also resembles *Ulmus* sp. 2 from the Bridge Creek flora, but tends to have a greater number of secondary vein pairs (12–18 vs. 10–14) (Meyer and Manchester 1997). Some of these leaves possess insect damage in the form of window feeding. Specimens UF 256-21275 and UF 256-84744 have a relatively long

petiole, 5.3 and 7.4 mm, respectively, compared to all the other *U. chuchuanus* specimens. Specimen UF 256-20753 may be an *Ulmus*, with a very young flower containing 4–5 distinct tepals, in the leaf axil. There are ~30 other *Ulmus*-like specimens but the finer venation is not preserved for identification to the species level. *Ulmus* is also represented by two species of well preserved silicified woods from the adjacent late Eocene Post Hammer and Dietz Hill sites (Wheeler and Manchester, 2007, 2021; Wheeler et al. 2023) (Table 3).

*Ulmus* consists of 25–37 species of trees found in North and Central America, temperate Eurasia to Northern Indo-China, and Northern Africa (Mabberley 1993, GBIF 2021, PoWO 2023).

*ULMUS OKANAGANENSIS* DENK & DILLHOFF, 2005

FIG. 3E, M

*Ulmus okanaganensis* Denk and Dillhoff, 2005, Can. J. Bot. 83, p. 1665, figs. 2–5.

**Referred specimens**—UF 256-20908–20911, 21120, 21141, 21244, 21274, 21276, 21283, 21288, 21292, 21294, 21299, 21303, 21319, 21349, 21535, 21554, 21559, 59184, 62697, 78825, 84742.

**Description**—Lamina elliptic or narrowly elliptic, unlobed, asymmetrical to symmetrical, nanophyll or small, length 17–73 mm ( $x=43$ ,  $N=12$ ), width 11–47 mm ( $x=24$ ,  $N=19$ ), l/w ratio 1.1–2.7, leaf area estimate 136–2000 mm<sup>2</sup> ( $x=775$ ,  $N=12$ ), petiole length 1–6 mm; lamina apex acute; base cuneate, symmetrical to highly asymmetrical; margin compound serrate, with two orders of teeth; teeth rounded to widely triangular, regularly spaced, usually distant, sometimes with short apiculate tip, distal flank sinuous, concave or straight, proximal flank straight or convex; sinuses angular; venation pinnate; midvein moderate to stout, straight to curved; secondary venation craspedodromous, 10–14 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 45–57°, middle to apical 41–67°, course straight to slightly curved, simple to frequently branched of 4–7 per side, rarely  $\frac{1}{2}$  to more frequently  $\frac{3}{4}$  distance to margin, exmedial branches of secondaries 1–3, to teeth and sinus; intersecondaries less than one per intercostal, extend rarely to  $> 1/2$  distance to margin, bifurcates at end or loops to subadjacent secondary; tertiary venation perpendicular to secondaries, reticulate to mixed percurrent; quaternary venation reticulate; areole polygonal. Fruit stipitate, lacking wing. Endocarp elliptic, length 3.5–4.5 mm ( $x=4.3$ ,  $N=4$ ), width 2.5–3.0 mm ( $x=2.8$ ,  $N=4$ ), with persistent style, length 1.5–2.0 mm ( $x=1.9$ ,  $N=4$ ); stipe 1–2.5 mm long ( $x=1.8$ ,  $N=3$ ); perianth length 2.5

mm, width 2.6 mm, situated below endocarp.

**Discussion**—We have placed isolated fruits and foliage specimens in the same species, because they match those found in mutual connection on twigs from the Eocene Princeton flora of British Columbia (Manchester 1989a, [Denk and Dillhoff 2005](#)). The leaves are consistent with *Ulmus okanaganensis* leaf type 1 (sensu [Denk and Dillhoff 2005](#)) in shape, lower number of secondary vein pairs, longer petiole, and tooth shape (Fig. 3E). They are also similar to the fossils assigned by Becker (1961) to *U. paucidentata* Smith (1939) from Ruby Basin and Beaverhead Basins floras (Table 2), except that *U. paucidentata* leaves are smaller and slender. The leaves are also similar to those of *Ulmus tenuinervis* Lesquereux (1878) from the Florissant flora, except *U. tenuinervis* leaves are ovate with an acuminate apex (Table 2). Some leaves possess insect damage in the form of window feeding. The associated fruit type, with persistent styles and lacking a pronounced wing (Fig. 3M), is similar to extant *Ulmus* section *Chaetoptelea* Liebmann (1850) ([Meyer and Manchester 1997](#), [Manchester 1999](#)). These fruits coincide with *U. okanaganensis* by a long stipe and wingless margin ([Denk and Dillhoff 2005](#)), and resemble *Ulmus* sp. A (sensu [Meyer and Manchester 1997](#)) from the Bridge Creek flora (Table 2).

*ULMUS* SP.

FIG. 3N

**Referred specimen**—UF 256-20907.

**Description**—Fruit stipitate with well-developed wing surrounding an elliptical endocarp; stigmatic notch present at apex of wing, with stigmatic arms; fruit body (minus stipe) 7 mm long, 5 mm wide, elliptical endocarp 4.5 mm long, 2.5 mm wide; stipe 2.8 mm long; wing with well-developed marginal vein, and prominent veins radiating out to wing margin.

**Discussion**—This species is distinguished from the co-occurring fruits of *Ulmus okanaganensis*, treated above, by the presence of a well-developed wing. The wing has a strong marginal vein and apical notch, and it surrounds an elliptical endocarp (Fig. 3N) as is typical of many species of extant *Ulmus* ([Manchester 1989a](#)). This specimen is similar to *Ulmus* sp. B from Bridge Creek (minus the persistent calyx), *U. tenuinervis* from Florissant, as well as the fruit found from the Whitecap Knoll flora (Table 2).

FAGALES ENGLER, 1892  
BETULACEAE GRAY, 1822  
*ALNUS* MILLER, 1754

*ALNUS NEWBERRYI* MEYER & MANCHESTER, 1997

FIG. 3F, G, U

*Alnus newberryi* Meyer and Manchester, 1997, Univ. Cal. Pub. Geol. Sci. 141, p. 93, pl. 27, figs. 1–4, pl. 28, figs. 1–3.

**Referred specimens**—UF 256-21064, 21066, 21068, 21069a, 21072, 21074, 21076–21078, 21080, 21081, 21085, 21087, 21089, 21093, 21097, 21098, 21101a, 21102, 21118, 21157, 21240, 21246, 21249, 21367–21369, 21372, 21413, 21490a, 21533, 21534, 21553, 21579b, 21600, 21601a, 21620, 34074, 34075, 34090, 56284, 59279a, 59280, 59281, 59282a,b, 59283, 59285, 59286, 59291, 59292, 59301, 78148, 78154, 78835–78838, 79031a, 87109, 87126.

**Description**—Lamina elliptic, widely elliptic, or slightly ovate, unlobed, symmetrical, small or notophyll, length 19–113 mm ( $x=47$ ,  $N=55$ ), width 10–58 mm ( $x=31$ ,  $N=56$ ), l/w ratio 1.1–2.3, leaf area estimate 117–3802 mm<sup>2</sup> ( $x=1960$ ,  $N=56$ ), petiole length up to 27 mm, width up to 1.7 mm; lamina apex acute to acuminate; base acute, obtuse, rounded, truncate, or cordate; margin compound serrate with 1–3 smaller teeth between secondaries; teeth regularly spaced, distant, primary teeth distal flank short, predominantly straight, occasionally concave, convex or flexuous, proximal flank attenuate, straight, convex or flexuous, apex broadly to rarely narrowly acute, secondary teeth distal flank predominantly straight, occasionally convex, proximal flank concave, apices rounded to acute; sinuses angular; venation pinnate; midvein weak or moderate, straight; secondary venation simple craspedodromous, basal minor secondaries semi-craspedodromous; 4–7 pairs, spacing regular, upper secondaries more acute than lower, angle of divergence basal 43–77°, middle 37–61°, apical 35–48°, course straight to slightly curved, sometimes near margin abrupt upward curve to teeth; 1–2 exmedial tertiary branches of distal portion of secondaries terminate in sinus or teeth, the lower exmedial tertiary joins at nearly right angles with tertiary vein nearly parallel to margin and arising from subadjacent secondaries; one admedial tertiary branching from distal secondaries terminate in sinus of major teeth; tertiary venation mixed percurrent, perpendicular to oblique from secondaries, angle of epimedial tertiaries 43–112°, distal course parallel to intercostal tertiaries; quaternary venation quadrangular to pentagonal; areoles well developed, veinlets absent to simple; marginal ultimate venation looped.

**Discussion**—Although leaves of different betulaceous genera can overlap in leaf architectural characters, the co-occurrence of this foliage with the woody infructescence diagnostic of *Alnus* Miller, described below, gives

additional confidence in the generic determination. These specimens are placed in *Alnus newberryi*, a species based on fossils from the Bridge Creek flora (Table 2). Specimen UF 256-21084 may be an aberrant form of *A. newberryi* due to the truncate base. *A. newberryi* also occurs in the Sumner Spring and Whitecap Knoll floras (Table 2).

For an example of an extant species similar to our specimens, we studied *Alnus oblongifolia* Torrey (1859), which is similar in its simple craspedodromous venation, serrate margin, percurrent tertiaries, tertiary vein near margin forming a loop, and veinlets absent to simple, but in *A. oblongifolia*, the secondaries are decurrent a short distance down the midvein and veinlets are usually branched. Leaf shape, apex, base, secondary vein endings, and tertiary veins ending in sinuses or teeth (Fig. 3F) are characteristic of Group 1-A of Klucking (1959) which includes *A. japonica* (Thunberg) Steudel (1840), *A. trabeculosa* Handel-Mazzetti (1922), and *A. cordata* (Loiseleur) Loiseleur (1828).

ALNUS SP. INFRACTESCENCE

FIG. 30

**Referred specimens**—UF 256-20915, 20916, 20917a,b, 20918.

**Description**—Cone-like infructescences, nearly orbicular to oblong, length 8–14 mm ( $x=11$ ,  $N=5$ ), width 5–7 mm ( $x=6$ ,  $N=5$ ); pedicel length 5 mm, width 1.1 mm. Infructescence consisting of helically arranged woody bracts.

**Discussion**—These infructescences (Fig. 30) resemble those of *Alnus* spp. from the Bridge Creek flora (Table 2) that may correspond to the leaves of *A. newberryi* (Meyer and Manchester 1997). They also resemble those associated with *Alnus clarnoensis* Liu, Manchester et Jin (2014) of the Eocene Clarno Formation (Table 2, Liu et al. 2014). *Alnus* infructescence is also represented in the nearby Late Eocene site of Post Hammer (Wheeler and Manchester 2021) (Table 3).

CARPINUS LINNAEUS, 1753

CARPINUS SP. FRUIT

FIG. 3P

**Referred specimen**—UF 256-21037.

**Description**—Winged fruit, with an ovate nutlet 2.0 mm long, at least 1.75 mm wide (partial width of incompletely preserved nutlet), borne at base of elongate, unlobed winglike bract; bract 11.0 mm long, at least 3.7 mm wide (partial width); primary veins four, craspedodromous, radiating from base and one side of bract and

extending to apex and teeth, width of veins decreasing exmedially; two exterior primary veins bifurcate less than  $\frac{1}{2}$  distance to apex, and rejoin apically forming cellular pattern; one secondary arising basal and exmedially to primary veins; two secondary veins arise from base and second side of bract, bifurcating less than  $\frac{1}{2}$  distance to apex, and rejoin apically forming cellular pattern; secondary veins alternate, produced from thickest primary vein; tertiary veins connecting middle primaries at acute angles; margin of two preserved distantly spaced teeth, vascularized by minor primaries; sinus rounded; basal pedicel 3.2 mm long, 1.4 mm wide.

**Discussion**—*Carpinus* fruits are quite rare in the fossil record of western North America (Manchester 1999). The incomplete nature of this specimen (Fig. 3P) does not allow for precise determination, but it resembles the extinct *Carpinus perryae* Pigg, Manchester and Wehr (2003) from the Middle Eocene of Republic Washington (Pigg et al. 2003) and *C. stenophylla* Nathorst (1883) from the Middle Miocene to late Pliocene of Japan (Tanai 1961). *Carpinus*-like leaves associated with the extinct fruit genus *Asterocarpinus* Manchester and Crane (1987), which have been reassigned to *Paracarpinus* Manchester and Crane (1987), are found in the Ruby Basin, York Ranch, Beaverhead Basins, Bridge Creek and Florissant floras (Table 2, Manchester and Crane 1987).

*Carpinus* consists of 26–43 extant species of trees found in temperate and subtropical Northern Hemisphere (Mabberley 1993, GBIF 2021, PoWO 2023).

CARPINUS/OSTRYA SCOPOLI, 1760

MORPHOTYPE TRL 08

FIG. 3H, V

**Referred specimens**—UF 256-21272, 21432, 21526.

**Description**—Lamina narrowly elliptic, symmetric, unlobed, nanophyll or small, length 16–53 mm ( $x=35$ ,  $N=3$ ), width 6–17 mm ( $x=12$ ,  $N=3$ ), l/w ratio 2.6–3.1, leaf area estimate 65–596 mm<sup>2</sup> ( $x=317$ ,  $N=3$ ), petiole missing; lamina apex attenuate; base acute, cuneate; margin compound serrate, with 1–2 smaller teeth between secondaries; teeth regularly spaced, distant, primary teeth distal flank short, straight to slightly convex or concave, proximal flank attenuate, sinuous to straight, apex acute; secondary teeth distal and proximal flanks straight, apices acute; sinuses angular; venation pinnate; midvein weak, straight; secondary venation craspedodromous, secondary pairs 15, irregular, angle of divergence decreasing apically, basal 43–62°, middle 36–57°, apical 32–44°, course slightly curved to sometimes sinuous; 1–2 exmedial minor secondary branches from distal

portion of secondaries and terminate in teeth; tertiary venation obscurely percurrent; higher order veins undistinguished; areoles well developed, pentagonal.

**Discussion**—These specimens are consistent with extant Betulaceae, particularly *Carpinus* and *Ostrya*, in characters of leaf shape, closely spaced, slightly curved secondaries and compound serrate margin (Fig. 3H). Leaves of both of these genera have secondary veins and agrophic veins terminating in the teeth but in *Carpinus* leaves the agrophic veins are confined mainly to the basal portion of the leaves while in *Ostrya* they occur also in the apical portion (Chaney 1927, Klucking 1959). The Teater Road specimens are poorly preserved in the apical portion, which is important in confirming relations with *Carpinus* or *Ostrya*, but they look especially similar in shape, teeth size, and secondary vein course to *Ostrya oregoniana* Chaney (1927) from the Bridge Creek flora (Chaney 1927, see plate 9, fig. 11, Meyer and Manchester 1997). The presence of *O. oregoniana* in the Beaverhead Basins flora is in question, as they have venation suggestive of Rosaceae (Table 2, Lielke et al. 2012).

CF. *CARPINUS*  
MORPHOTYPE TRL 09

FIG. 3I, J

**Referred specimen**—UF256-21244, 87130.

**Description**—Lamina apparently ovate, unlobed, partial length 60 mm, partial width 48 mm; l/w ratio 1.7, petiole missing; apex missing, base angle acute, shape cuneate; margin simple to compound serrate, basal portion of lamina with simple teeth of relatively similar size, upper portion of lamina compound serrate with 1 to possibly 2 smaller teeth between secondaries; teeth irregularly spaced, distant, apices acute, distal flank straight to sometimes shallow concave, proximal flank straight to shallow convex; sinuses angular; venation pinnate; midvein straight; secondary venation craspedodromous, secondary pairs at least 7, irregular, angle of divergence decreasing apically, basal 60–62°, apically 51–54°, course straight to near margin then curved apically; 2–4 exmedial minor secondary branches from distal portion of secondaries and terminate in teeth; tertiary venation mixed percurrent; epimedial tertiaries nearly right angle to midvein; quaternary venation reticulate; areoles well developed.

**Discussion**—This specimen is distinguished from the preceding species in base shape, and prominence of the teeth. It resembles leaves of *Carpinus caroliniana* Walter (1788) in features of marginal serration, and venation. As in *C. caroliniana*, secondary veins near the margin are

deflexed slightly into the tooth.

FAGACEAE DUMORTIER, 1829  
*QUERCUS* LINNAEUS, 1753  
*QUERCUS BERRYI* TRELEASE, 1918

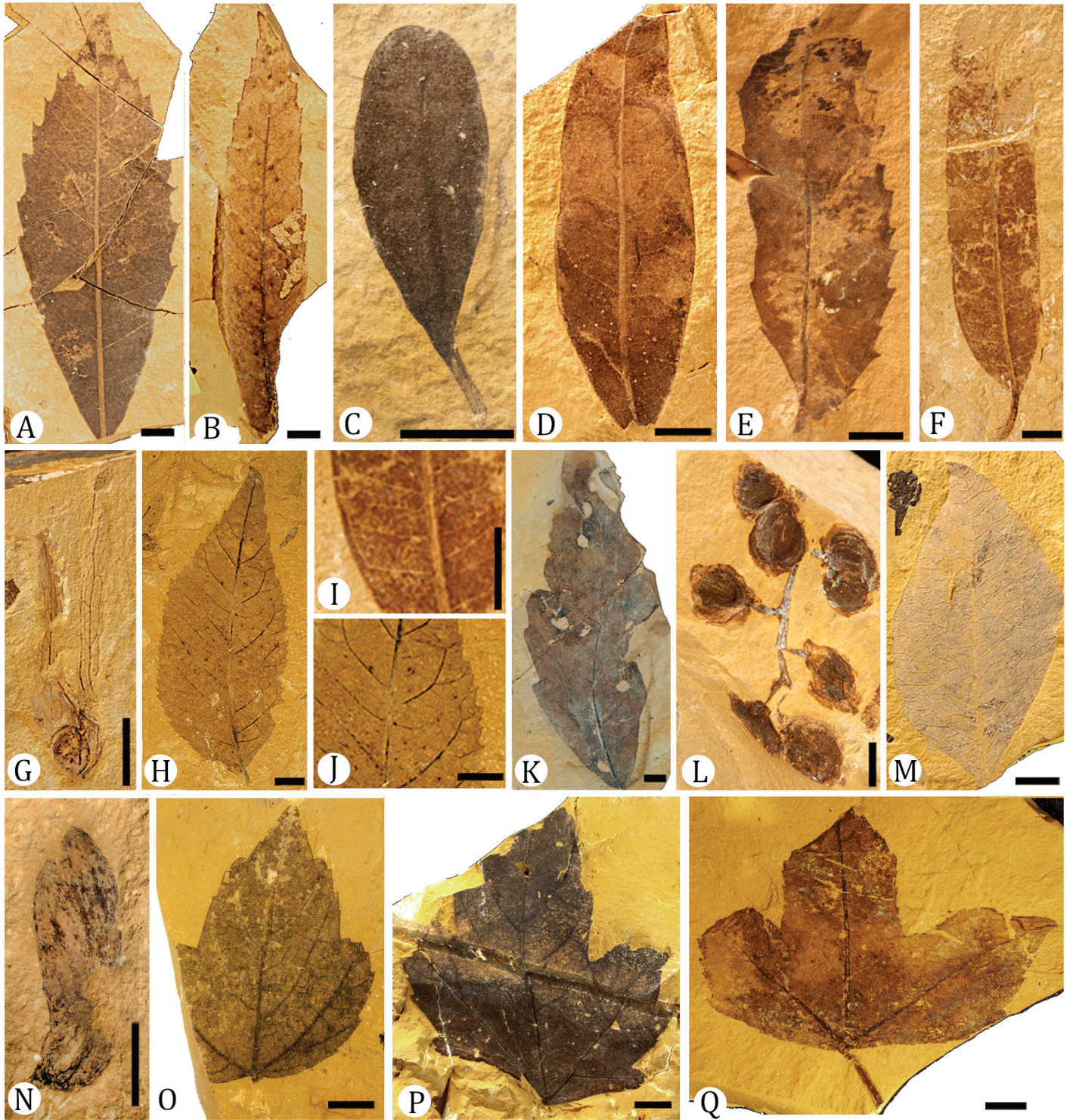
FIG. 4A, B

*Quercus berryi* Trelease, 1918, *pro parte*, Brooklyn Bot. Gard. Mem. 1, p. 499.

*Quercus breweri* auct. non Engelmann, Lesquereux, 1883, *pro parte*, Rept., U.S. Geol. Surv. Terr. 8, p. 246, pl. 54, fig. 9 only.

**Referred specimens**—UF 256-20695c, 21070, 21374, 21376, 21378–21383, 21385, 21386, 21388a, 21389, 21390–21394, 21395, 21396a,b, 21399–21408, 21410, 21411, 21415, 21416a,b, 21417a, 21419–21421, 21425, 21427–21430, 21436, 21437, 21439, 21440, 21443–21446, 21448, 21449, 21451–21457, 21459, 21461, 21462, 21464, 21466–21472, 21473a, 21474a, 21476a–21478a, 21481–21488, 21491–21495, 21497, 21498, 21501–21503, 21505, 21506, 21508a, 21509, 21512a, 21513, 21514, 21516–21518a, 21519a, 21520–21524, 21527, 21528, 21530, 21532, 21562, 21587, 21604, 21615, 21617, 21624, 34065, 34108, 59360–59365, 59367–59375, 59608, 59609, 59610a, 59611, 59612, 59614–59620, 59621a, 59622–59626, 59628, 59629, 78813–78816, 78819, 78820, 79030, 84738, 84752, 87124.

**Description**—Lamina elliptic, narrowly elliptic, or rarely obovate, symmetrical, unlobed, nanophyll or small, length 13–98 mm ( $x=48$ ,  $N=88$ ), width 6–30 mm ( $x=13$ ,  $N=163$ ), l/w ratio 1.9–6.6, leaf area estimate 49–1498 mm<sup>2</sup> ( $x=441$ ,  $N=88$ ) petiole length 1–5 mm, normal to inflated at base; lamina apex acute or attenuate, rarely truncate; base cuneate or slightly rounded; margin serrate, often serrate in upper lamina and entire at basal ¼ to ½ lamina length, occasionally entire throughout lamina; teeth regularly spaced, distant, apices acute, distal flank concave to straight, proximal flank convex to straight and attenuate; sinus rounded to angular; venation pinnate; midvein moderate to massive, straight or slightly curved; secondary venation in entire portion of leaf brochidodromous to eucamptodromous, in serrate portion craspedodromous, 10–15 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 36–62°, middle 43–65°, apical 43–53°, course straight to curved; intersecondaries rare or absent, extending < ½ distance to margin or near margin before joining tertiaries; tertiary venation reticulate to rarely alternate percurrent, acute to right angle with secondary veins; epimedial tertiaries nearly right angle to midvein;



**Figure 4.** **A.** *Quercus berryi* Trelease, UF 256-21468. **B.** *Q. berryi*, UF 256-21439. **C.** *Quercus pollardiana* (Knowlton) Axelrod, UF 256-21377. **D.** *Quercus* sp. 1, UF 256-21531b. **E.** *Quercus* sp. 2, leaf with craspedodromous secondaries and prominent teeth, UF 256-21529. **F.** *Decodon* sp., UF 256-21499. **G.** *Palaeocarya* sp., UF 256-20847. **H.** *Juglandiphyllites cryptatus* (Knowlton) Meyer and Manchester; UF 256-21146. **I.** *Decodon* detail from **F.** **J.** *Juglandiphyllites* detail from **H.** **K.** *Rhus lesquereuxii* Meyer and Manchester, UF 256-21540. **L.** *Toxicodendron* sp. 1, infructescence, UF 256-20752. **M.** *Toxicodendron* sp. 2 leaflet, UF 256-21607. **N.** *Loxopteroides weeksae* Manchester and Judd, UF 256-21048. **O.** *Acer clarnoense* Wolfe and Tanai, UCMP 9010A. **P.** *Acer clarnoense* Wolfe and Tanai, UF 256-21127. **Q.** *Acer* sp. 1 leaf, UF 256-21128. Scale bars: **A–K, M, O–Q**=5 mm; **L, N**=2 mm.

quaternary venation reticulate; fimbrial vein present.

**Discussion**—Serrate leaves with basal portion of the lamina entire can be found in Fagaceae, such as *Lithocarpus* Blume (1825), *Castanea* Miller (1754), and *Quercus*, while a fimbrial vein is found in *Quercus* and rarely *Castanea* (Meyer and Manchester 1997). Also, secondary veins in *Castanea* are straight, parallel, and may be forked before terminating into the teeth while the course of secondary veins in *Quercus* are variable (Smiley and Huggins 1981). For an example of an extant species similar to our specimens, we selected *Q. mohriana* Buckley ex Rydberg (1901) of south-central North America, in which the apical portions of the lamina may be toothed or can be completely entire, and the tertiary venation is predominantly reticulate. The difference is that *Q. mohriana* has fewer teeth, and teeth orientation varies from nearly perpendicular to apically pointed. Leaf architectural characters such as size, shape, margin, small petiole, number of secondary vein pairs, and reticulate tertiary venation of these fossil specimens (Fig. 4A, 4B) are similar to *Q. berryi* Trelease (1918) from the Bridge Creek flora (Meyer and Manchester 1997). *Quercus berryi* is highly variable in size, shape, leaf width and margin, but in our specimens with serrate margins, are similar in lower portion of leaf entire, tertiary veins reticulate, higher order veins form a fine reticulum, rare intersecondaries, and a fimbrial vein on the margin. These leaves are also similar to *Q. scudderi* Knowlton (1916) from the Florissant flora (MacGinitie 1953, see pl. 30, fig. 1, Manchester 2001) and *Q. simulata* Knowlton (1898) from the Beaverhead Basins flora (Table 2). Specimen UF 256-79029 is similar to *Q. berryi* except a few percurrent tertiaries near the margin send a branch to the teeth. *Quercus* has at least 26 fossil species spread across selected sites of western United States (Table 2).

*Quercus* consists of 400–600 species of trees and shrubs, is widespread in the Northern Hemisphere and extends to Malesia and Colombia (Mabberley 1993, Meyer and Manchester 1997, Manchester 1999, GBIF 2021).

*QUERCUS POLLARDIANA* (KNOWLTON) AXELROD, 1940

FIG. 4C

*Quercus pollardiana* (Knowlton) Axelrod, 1940, J. Wash. Acad. Sci. 30, p. 171–172.

*Chrysobalanus pollardiana* Knowlton, 1900, U.S. Geol. Surv. Ann. Rept. 21, p. 216, pl. 30, fig. 19.

**Referred specimens**—UF 256-21377, 21422, 21489, 21591, 78818, 79034.

**Description**—Lamina obovate or oblanceolate, symmetrical or asymmetrical, unlobed, nanophyll or small,

length 13–61 mm ( $x=32$ ,  $N=5$ ), width 5–31 mm ( $x=14$ ,  $N=5$ ), l/w ratio 1.6–3.0, leaf area estimate 46–1280 mm<sup>2</sup> ( $x=427$ ,  $N=5$ ), petiole length 1–4 mm; lamina apex rounded, sometimes emarginate; base cuneate; margin entire; venation pinnate; midvein stout, straight; secondary venation brochidodromous, 4–8 pairs, irregularly spaced, excurrent attachment, angle of divergence 42–56°, curved and slightly sinuous; higher order venation not preserved.

**Discussion**—These specimens conform to *Quercus pollardiana* in the rounded apices, cuneate base, entire margin, short and thick petiole (Fig. 4C), and possibly coriaceous texture, although rounded apices are relatively rare in *P. pollardiana* (Axelrod 1995). These specimens resemble those that were assigned to *Quercus dayana* Knowlton (1902) found in the Beaverhead Basins and Miocene floras of the Columbia Plateau (Chaney and Axelrod 1959), but the number of secondary vein pairs are 7–15 (Table 2).

*QUERCUS* SP. 1

FIG. 4D

**Referred specimens**—UF 256-21423, 21431, 21438, 21475a, 21531b, 21602, 59627, 76957.

**Description**—Lamina narrowly elliptic, symmetrical, unlobed, small, length 26–37 mm ( $x=30$ ,  $N=3$ ), width 7–19 mm ( $x=11$ ,  $N=9$ ), l/w ratio 2.5–3.2, leaf area estimate 141–291 mm<sup>2</sup> ( $x=192$ ,  $N=3$ ), petiole missing; lamina apex sharply acute to rounded; base acute, symmetrical to asymmetrical; margin entire; venation pinnate; midvein stout, straight; secondary venation brochidodromous, 6–10 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 65–86°, middle 32–52°, apical 43–51°, course arching apically from midvein or nearly perpendicular to midvein before arching apically; usually 1–2 intersecondaries per intercosta, extending < ½ distance or to near margin and merging with subadjacent secondaries, or tertiary veins; tertiary venation mostly reticulate; occasional epimedial tertiaries perpendicular to midvein; quaternary venation reticulate and polygonal; marginal vein present.

**Discussion**—For examples of extant species similar to our specimens, we selected *Quercus elliptica* Née (1801) and *Q. laurifolia* Michaux (1801) which are similar in size, apex and base shape, entire margin, brochidodromous secondary venation, usually one intersecondary that extends more than half the distance to the margin before merging with subadjacent secondaries, reticulate tertiaries, and presence of a marginal vein. *Quercus* sp. 1 differs from entire-margined *Q. berryi* in the strength

and number of intersecondary veins (Fig. 4D). These specimens seem close to *Q. convexa* Lesquereux (1878) in shape, margin, and venation but there is no indication of intersecondary veins, and the apices are usually rounded in *Q. convexa*. *Quercus convexa* are found in numerous Neogene floras of western North America (LaMotte 1952) with good examples in the Ruby Basin and Beaverhead Basins floras (Table 2).

*QUERCUS* SP. 2

FIG. 4E

**Referred specimens**—UF 256-21529, 21555a, 84724.

**Description**—Lamina elliptic, symmetrical or asymmetrical, unlobed, small, length 34–54 mm ( $x=44$ ,  $N=2$ ), width 13–14 mm ( $x=13$ ,  $N=3$ ), l/w ratio 2.5–4.3, leaf area estimate 303–451 mm<sup>2</sup> ( $x=377$ ,  $N=3$ ), petiole length 9 mm; lamina apex acute; base acute, asymmetrical; margin serrate; teeth simple, irregularly spaced, distant, apices acute or rounded, distal flank straight or concave, proximal flank straight or slightly convex; sinus rounded; venation pinnate; midvein moderate to stout, straight; secondary venation craspedodromous, at least 17 pairs, regular spacing, excurrent attachment, angle of divergence 40–65°, course straight to slightly curved; few percurrent tertiary veins preserved.

**Discussion**—These specimens are similar to *Quercus brooksii* Becker (1961) from the Ruby Basin flora (Table 2) with a distinct asymmetrical base, sharp teeth, and long petiole (Fig. 4E) but *Q. brooksii* has distinct percurrent tertiary veins and a flaring petiole base.

*QUERCUS* SP. 3

FIG. 7Q

**Referred specimen**—UF 256-21061.

**Description**—Mature fruit and immature cupule; nut widely elliptic, length 6–9 mm, width 4–8 mm; apex obtuse; base truncate and with circular, concave abscission scar; fruit surface with prominent, basal, longitudinal striations; immature cupule nearly enclosing fruit, length 4.1 mm, width 4.0 mm.

**Discussion**—This specimen seems to be an isolated mature fruit and immature cupule by orientation of the abscission scar (Fig. 7Q). We tentatively place this specimen in *Quercus* but would need cupule scale characters to distinguish between *Quercus* with helically arranged scales, and *Lithocarpus* with scales in concentric circles (Meyer and Manchester 1997). We would also need more specimens to see if the abscission scar is convex or more often deeply concave as in *Lithocarpus*, or are they mostly convex or flat, rarely deeply concave as in *Quercus* (Mu

et al. 2015). *Quercus* acorns have also been found in the Bridge Creek flora and in the Clarno Formation (Table 2, Meyer and Manchester 1997, Manchester 1994).

JUGLANDACEAE DE CANDOLLE EX PERLEB, 1818  
*JUGLANDIPHYLLITES* BOULTER & KVAČEK, 1989  
*JUGLANDIPHYLLITES CRYPTATUS* (KNOWLTON) MEYER & MANCHESTER, 1997

FIG. 4H, J

*Juglandiphyllites cryptatus* (Knowlton) Meyer and Manchester, 1997, Univ. Cal. Pub. Geol. Sci. 141, p. 101–102, pl. 33, figs. 3–6, pl. 34, figs. 1, 4.

*Juglans cryptata* Knowlton, 1902, U.S. Geol. Surv. Bull. 204, p. 35, pl. 6, figs. 4, 5.

**Referred specimens**—UF 256-20747b, 21137–21140, 21142–21147, 21148a,b, 21149, 21151, 21308, 21597, 34095, 34099, 34100, 34101.

**Description**—Leaflet ovate, elliptic, narrowly elliptic, or rarely obovate, asymmetrical, unlobed, small or rarely nanophyll, length 21–62 mm ( $x=45$ ,  $N=15$ ), width 11–37 mm ( $x=20$ ,  $N=21$ ), l/w ratio 1.4–4.3, leaflet area estimate 196–1525 mm<sup>2</sup> ( $x=625$ ,  $N=15$ ), petiolule length 2–8 mm; lamina apex acute; base cuneate or rounded, and asymmetrical; margin compound serrate with 1–2 orders of teeth, with 1–3 teeth between secondaries; teeth usually regularly spaced, distant, apices acute, distal flank straight to slightly concave, proximal flank straight, concave, convex or flexuous; sinuses angular or rounded; venation pinnate; midvein moderate or stout, straight to curved; secondary venation simple to compound craspedodromous and occasionally semicraspedodromous, 9–12 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 50–95°, middle 45–90°, apical 42–90°, course curved slightly to distinctly sinuous; 1–2, rarely four craspedodromous secondaries per leaf fork at more than ½ distance to margin, entering teeth medially; semicraspedodromous secondaries lose strength near margin and loop to superadjacent secondaries as strong to normal tertiary veins, marginal tertiary veins branch from these loops and enter teeth medially; occasionally 1–3 successive exmedial tertiary branches of distal secondaries terminate medially in teeth or sinus; less than one intersecondary per intercostal, extending mostly  $\leq$  ½ distance to margin before sometimes losing strength and joining subadjacent secondary, or percurrent tertiaries; tertiary venation mixed percurrent, right to acute angled from secondaries, sometimes marginal percurrent tertiary produces a branch to a tooth; epimedial tertiaries nearly right angle to midvein, distal course parallel to intercostal tertiaries; quaternary venation composed of

fine, well developed pentagonal or orthogonal areoles; one branched free ending veinlets sometimes present.

**Discussion**—These specimens conform to Juglandaceae by their asymmetrical leaflets with craspedodromous to semicraspedodromous venation, strong percurrent tertiaries, venation entering teeth medially, and the fine network of quaternary areoles (Fig. 4H). Within extant Juglandaceae, species of *Oreomunnea* Oersted (1856) and *Alfaroa* Standley (1927) with serrate margined leaflets, can be distinguished by the course of the secondary veins as they enter the teeth, often contacting the sinus and paralleling the apical flank. In *Engelhardia* Leschenault ex Blume (1825) leaflets with serrate margins, the teeth are rounded, and veinlets are free ending (Manchester 1987b). The leaf architecture of these fossils resembles that of extant *Carya* Nuttall (1818), *Juglans* L. (1753) and *Pterocarya* Kunth (1824) (Manchester 1987b, Meyer and Manchester 1997). In *Juglans*, secondary veins are brochidodromous; in some species (those of subg. *Rhysocaryon* Dode, 1909) the tertiary veins enter the apical side of the teeth or end in the sinuses, whereas in subg. *Cardiocaryon* Dode (1906) veins enter the teeth medially. In *Pterocarya*, secondary veins loop apically near the margin, joining the superadjacent secondary without prominent forking (Meyer and Manchester 1997). The irregular course of the secondaries near the margin fits with *Juglandiphyllites cryptatus* from the Bridge Creek flora (Table 2). Silicified wood of *Pterocaryoxylon* Müller-Stoll and Mädler (Wheeler and Manchester 2021) and *Carya* (Wheeler et al. 2023) and fruits of *Carya* and *Juglans* occur in the nearby late Eocene Post Hammer and Dietz Hill sites (Wheeler and Manchester 2021, Wheeler et al. 2023, Manchester and McIntosh 2007; personal observation) (Table 3). At Teater Road, two compressed fruits, UF 256-21000 and UF 256-21400, are similar to *Juglans clarnensis* Scott (1954) (Manchester 1987b) in size and 4–5 longitudinal, shallow, parallel furrows present on one face, but lack of internal characters precludes precise determination. Whether *J. cryptatus* represents *Carya*, *Juglans*, *Pterocarya* or an extinct genus remains uncertain. Fruits and foliage of *Carya* are confirmed from the Florissant flora (Table 2, MacGinitie 1953, Manchester 1987b). In addition, possible foliage and/or nuts attributed to *Carya* and *Juglans* are found in Whitecap Knoll, York Ranch, Beaverhead Basins, and Bridge Creek floras (Table 2).

*PALAEOCARYA* SAPORTA, 1873 EMEND. MANCHESTER 1987B  
*PALAEOCARYA* SP.

FIG. 4G

**Referred specimen**—UF 256-20847.

**Description**—Fruit a winged nutlet with tri-lobed wings, wing lobes lanceolate; central lobe length 18 mm (incomplete due to edge of specimen), width 2.5 mm, lateral lobe length 15 mm, width 2.5 mm; lobes with primary and at least one lateral, parallel, ascending veins; primary and lateral veins with interior secondaries veins at right to acute angles, with straight, ascending tertiary veins and also sinuous tertiary veins at right angles enclosed by interior secondaries and primary/lateral veins; lateral vein with exmedial loops of secondary veins, and marginal loops of tertiary veins; prophyllum, entire, ovate, length 5 mm, width 2.75 mm; nutlet oval, length 3.8 mm, width 3.1 mm; pedicel missing.

**Discussion**—The tri-lobed bract of this fruit (Fig. 4G) is diagnostic of Juglandaceae, Tribe Engelhardieae, genera *Engelhardia* and *Oreomunnea* (Manchester 1987b). The incompleteness of this specimen makes precise identification difficult, but characters of the wings, prophyllum and nutlet suggest *Palaeocarya* Section *Palaeocarya* Manchester (1987) (Manchester 1987b, Meyer and Manchester 1997). *Palaeocarya* fruits are also found in the Clarno Formation, Sumner Spring, Whitecap Knoll, and Bridge Creek floras (Table 2).

*Engelhardia* and *Oreomunnea* are distributed within tropics regions, *Engelhardia* from India to New Guinea, and *Oreomunnea* from Mexico to Colombia (Meyer and Manchester 1997, GBIF 2021, PoWO 2023).

MYRTALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820  
LYTHRACEAE J. SAINT-HILAIRE, 1805  
*DECODON* J.F. GMELIN, 1791  
*DECODON* SP.

FIG. 4F, I

**Referred specimens**—UF 256-21409, 21460, 21480, 21499, 34106, 78832a, 84600.

**Description**—Lamina lanceolate to linear, symmetrical to asymmetrical, unlobed, small, estimated length 43–69 mm ( $x=55$ ,  $N=5$ ), width 10–26 mm ( $x=14$ ,  $N=7$ ), l/w ratio 4–7, leaf area estimate 340–501 mm<sup>2</sup> ( $x=410$ ,  $N=5$ ); petiole length 6–13 mm ( $N=2$ ); lamina apex missing; base cuneate; margin entire; venation pinnate; midvein moderate to stout, straight; secondary venation brochidodromous such that the exmedial loops form a slightly wavy intramarginal vein, ~13 pairs, irregularly spaced, excurrent attachment, angle of divergence 60–90°, course straight to near margin or straight to nearly ½ distance to margin then curve apically; usually one intersecondary per intercosta, sometimes extending to near intramarginal vein before branching at right angles

and joining adjacent secondaries; tertiary venation poorly preserved.

**Discussion**—The architecture of this leaf type resembles that of extant *Decodon verticillatus* (L.) Elliott (1821), characterized by brochidodromous venation, an intramarginal vein formed by a series of arches of the secondary veins, and intersecondaries that extend to near the intramarginal vein before branching at right angles and joining adjacent secondaries (Wolfe and Tainai 1980). Our specimens are also similar to *D. brownii* Meyer and Manchester (1997) from the Bridge Creek flora characterized by a slightly wavy intramarginal vein (Table 2, Meyer and Manchester 1997), but the tertiary venation is too poorly preserved for specific assignment (Fig. 4F). *Decodon* leaves have also been observed in Sumner Spring, Whitecap Knoll (Table 2), and Badger's Nose floras (Myers 2006). The genus is also confirmed by permineralized fruits from the Clarno Nut Beds (Table 2, Manchester 1994).

*Decodon* consist of one extant species, found in swamps of Eastern Canada to Central and Eastern United States (Mabberley 1993, GBIF 2021, PoWO 2023).

SAPINDALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820  
ANACARDIACEAE R. BROWN, 1818B  
RHUS LINNAEUS, 1753  
RHUS LESQUEREUXII MEYER & MANCHESTER, 1997

FIG. 4K

*Rhus lesquereuxii* Meyer and Manchester, 1997, Univ. Cal. Pub. Geol. Sci. 141, p. 129, pl. 51, figs. 5, 6, pl. 52, figs. 1–5.

**Referred specimens**—UF 256-21088, 21477, 21540–21543, 21614a, 34123, 78149.

**Description**—Lamina lanceolate, asymmetric, unlobed, small or notophyll, estimated length 58–92 mm ( $\bar{x}=79$ ,  $N=3$ ), width 16–37 mm ( $\bar{x}=25$ ,  $N=10$ ), l/w ratio 2.5–2.7, leaf area estimate 861–2241 mm<sup>2</sup> ( $\bar{x}=1632$ ,  $N=3$ ), petiole missing; lamina apex acute; base cuneate, asymmetrical; margin serrate in upper 2/3 leaf length, simple, teeth large, irregularly spaced, distant, apices rounded, distal flank slightly convex, proximal flank convex to straight and attenuate; sinuses acute, usually fed by an exmedial branch of the secondary vein; venation pinnate; midvein moderately thick, curved; secondary venation craspedodromous and eucamptodromous, ~11–13 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 42–72°, middle 46–66°, apical 46–52°, course straight to more than 1/2 distance to margin then curved apically in basal portion of lamina, curved in apical portion of lamina, sometimes branched and joining

superadjacent secondary; less than one intersecondary per intercosta, extending about 1/2 distance to margin; tertiary venation free ramified to occasionally percurrent; quaternary venation irregular reticulate and closely spaced; free ending veinlets mostly absent.

**Discussion**—These specimens conform to Anacardiaceae; for example, resembling *Rhus glabra* L. (1753), characterized by relatively large teeth, sinuses usually fed by abaxial branching of secondaries, and transversely free ramified to occasionally percurrent tertiaries. These specimens conform to *R. lesquereuxii* Meyer and Manchester (1997) from the Bridge Creek flora (Table 2, Meyer and Manchester 1997, see pl. 52, fig. 1) in lamina size, tooth shape, base symmetry, exmedial branching to sinuses, and transverse tertiaries (Fig. 4K). *Rhus lesquereuxii* from the Florissant flora (Table 2, MacGinitie 1953) has sharp pointed teeth. Additional *Rhus* species have been found including an endocarp from the Clarno Nut Beds and leaflets from Bridge Creek, Beaverhead Basin, Badger's Nose (Myers 2006), Metzel Ranch, York Ranch, Green River, and Florissant floras (Table 2). Some of these specimens are superficially similar to lobed *Quercus* leaves, but they lack a marginal vein usually found in *Quercus*, and *Quercus* seems to lack transversely free ramified tertiary veins (Luo, Y. and Z-K. Zhou. 2002).

*Rhus* includes 35–54 species of shrubs and small trees, found in warm and temperate regions throughout the world (Mabberley 1993, Yi et al. 2004, GBIF 2021, PoWO 2023).

TOXICODENDRON MILLER, 1754  
TOXICODENDRON SP. 1

FIG. 4L

**Referred specimens**—UF 256-20752, 84754, 84755.

**Description**—Fragment of a racemose infructescence, length 8 mm, with alternate arranged pedicellate fruits; pedicel length 1–1.2 mm, width 0.3–0.4 mm; fruits circular or oblate, length 2.8–5.6 mm, width 2.0–3.8 mm, with persistent calyx base and stigma; outer wall thin; fruits appear to be glabrous; endocarp with longitudinal grooves.

**Discussion**—These specimens conform to *Toxicodendron*, characterized by the presence of a racemose infructescence, small fruits with a thin outer wall, longitudinal grooved endocarps, with persistent calyx base and stigma (Fig. 4L). Similar fruits are found in *Rhus* but they are in a paniculate arrangement, and the stigma can sometimes be divided into two lobes. *Toxicodendron* is also found in the Bridge Creek and Green River floras (Table 2).

*Toxicodendron* consists of 15–28 species of shrubs

and climbers, found in Canada to southwestern South America, Pakistan to Eastern Asia and to Sumatra (Maberley 1993, Meyer and Manchester 1997, GBIF 2021, PoWO 2023).

CF. *TOXICODENDRON* MILLER, 1754

FIG. 4M

**Referred specimen**—UF 256-21607.

**Description**—Lamina ovate, small, unlobed, length 37 mm, width 20 mm, l/w ratio 1.8, leaf area estimate 494 mm<sup>2</sup>, petiole missing; lamina apex and base acute; margin entire; venation pinnate; midvein moderately thick; secondary venation cladodromous and extending to margin; tertiary venation transversely ramified, sometimes reaching margin, some alternate percurrent; higher order venation not preserved; surface punctate.

**Discussion**—This specimen is similar to *Toxicodendron wolfei* Meyer and Manchester (1997) from the Bridge Creek flora (Table 2), characterized by an entire margin leaf with cladodromous secondary veins and transversely ramified to percurrent tertiary veins (Fig. 4M). The difference is that the Teater Road specimen is quite small and the surface is punctate (Meyer and Manchester 1997). While leaves of extant species of *Rhus* and *Toxicodendron* lack punctate leaf surfaces, *Garcinia livingstonei* T. Anderson (1867) (Clusiaceae) does have a punctate surface, entire margin and mixed brochidromous/cladodromous venation, although the leaf shape is elliptic to obovate and are typically about twice as large as our specimen.

*LOXOPTEROIDES* MANCHESTER & JUDD, 2022

*LOXOPTEROIDES WEEKSAE* MANCHESTER & JUDD, 2022

FIG. 4N

*Loxopteroides weeksae* Manchester and Judd, 2022, *Acta Palaeobot.* 62, p.3, Pl. 1, figs. A–O.

**Referred specimen**—UF 256-21048.

**Discussion**—A single samara (Fig. 4N) in the Teater Road collection represents the youngest known occurrence of the extinct anacardiaceous genus *Loxopteroides* which was initially described based on specimens from the Middle Eocene of Oregon and California (Table 2, Manchester and Judd 2022). In addition to the three representatives of Anacardiaceae treated here, the distinctive wood of *Pistachia* has been identified among silicified woods from the nearby late Eocene Post Hammer site (Wheeler and Manchester 2023) (Table 3).

MELIACEAE JUSSIEU, 1789

*CEDRELA* P. BROWNE, 1756

*CEDRELA MERRILLII* (CHANNEY) BROWN, 1937

FIG. 6U

*Cedrela merrillii* (Chaney) Brown, 1937, *Wash. Acad. Sci. J.* 27, p. 511–512.

*Rhus merrillii* Chaney, 1927, *Carnegie Inst. Wash. Publ.* 346, p. 125, pl. 16, figs. 1, 2.

**Referred specimens**—UF 256-20807, 20808, 21044, 21050.

**Description**—Winged seed, elliptic, length 9–16 mm ( $x=12$ ,  $N=4$ ), width 4.1–5.5 mm ( $x=5$ ,  $N=4$ ), wing extending laterally from seed body; apex acute or obtuse; base acute; proximal margin straight, distal margin shallow convex; wing base sometimes extending around seed body in narrow strip; wing with single vein emerging from distal side of seed body, then arching upward to near apex along proximal margin, then sometimes looping back down just inside of distal margin; wing with distinct polygonal cells; seed body oval, length 4.1–5.2 mm ( $x=4.8$ ,  $N=3$ ), width 2.9–3.2 mm ( $x=3.0$ ,  $N=3$ ).

**Discussion**—The aforementioned characters are similar to the extant genus *Cedrela* Browne and conform to the fossil species *Cedrela merrillii* from the Bridge Creek flora. Leaflets of *Cedrela lancifolia* (Lesquereux) Brown (1937) are present in Ruby Basin, Beaverhead Basins, and Florissant floras. *Cedrela pteriformis* (Berry) Brown (1935), a winged seed with a hooked shaped distal margin (Brown 1935), is present in Metzel Ranch and Beaverhead Basins floras, and *C. trainii* Arnold (1936), a lanceolate leaflet, is present in the Sucker Creek flora (Arnold 1936b) (Table 2).

*Cedrela* includes 19 extant species of shrubs and trees, found in Mexico to tropical America (GBIF 2021, PoWO 2023).

RUTACEAE JUSSIEU, 1789

*RUTASPERMUM* CHANDLER EMEND. GREGOR, 1975

*RUTASPERMUM* SP.

FIG. 6E

**Referred specimen**—UF 256-21051, 21053, 21054, 62694, 84911.

**Description**—Seed oval, length 3.4–4.6 mm ( $x=3.8$ ,  $N=5$ ), width 3–3.2 mm ( $x=3.1$ ,  $N=5$ ); hilar surface with numerous pits, non-hilar surface marked with a reticulum of longitudinal and smaller rugulae, interspersed with numerous pits; hilar scar elongate.

**Discussion**—We tentatively placed these distinctive specimens in the form genus *Rutaspermum* due to the overlap among seeds of different modern genera. These specimens are similar to extinct *Rutaspermum meselense* Collinson and Gregor (1988) and *Zanthoxylum*

*rhabdospermum* (Lesquereux) Tiffney (1980) (Collinson and Gregor 1988, Tiffney 1980). The Teater Road species (Fig. 6E) is very similar to that designated as “*Rutaspermum* undetermined B” from the Middle Eocene Messel flora of Germany (Pl. 37, figs g-i in Collinson et al 2012).

SAPINDACEAE JUSSIEU, 1789  
ACER LINNAEUS, 1753

Wolfe and Tanai (1987) recognized seven species of *Acer* from the Teater Road locality, which they called Sheep Rock Creek, based on leaves and fruits: *Acer beckii* Wolfe and Tanai, *A. crookense* Wolfe and Tanai), *A. meyeri* Wolfe and Tanai, *A. ovipetrinum* Wolfe and Tanai, *A. sinuofluviatilis* Wolfe and Tanai, *A. clarnoense* Wolfe and Tanai, and *A. postense* Wolfe and Tanai. Here we review those species with the benefit of some additional specimens collected subsequent to Wolfe and Tanai’s work. We conclude that *Acer beckii* and *A. meyeri* are synonyms, for which we retain the name *A. meyeri*. Some of Wolfe and Tanai’s species included both fruits and leaves under the same epithet, but without clear evidence. Herein we recognize eight species, two based only on leaves and six based only on fruits. We lack clear evidence to determine which fruit species belong to the species known from leaves. *Acer* is widespread within our selected sites of western North America (Table 2). *Acer* is also represented by two species of silicified wood from the nearby Late Eocene Post Hammer site (Wheeler and Manchester 2021) (Table 3).

*Acer* consists of 100–153 extant species of trees, found in temperate areas and tropical mountains of the Northern Hemisphere (Mabberley 1993, GBIF 2021, PoWO 2023).

ACER CLARNOENSE WOLFE & TANAI, 1987 EMEND. LOTT & MANCHESTER

FIG. 40, P

**Basionym**—*Acer clarnoense* Wolfe and Tanai, 1987, *pro parte*, J. Fac. Sci., Hokkaido Univ. 22, p. 78–79, pl. 14, figs. 5–7 only.

**Holotype**—UCMP 9010A.

**Paratypes**—UCMP 9011, 9012.

**Referred specimens**—UF 256-21127, 21259, 21260, 21261, 34071a.

**Emended description**—Lamina widely to very widely ovate, mostly shallowly trilobed, small or notophyll, length 29–63 mm ( $x=45$ ,  $N=5$ ), width 24–62 mm ( $x=38$ ,  $N=5$ ), l/w ratio 0.9–1.6, leaf area estimate 476–2286 mm<sup>2</sup> ( $x=1243$ ,  $N=5$ ), petiole missing; lamina apex acute; base round to truncate; lobe apices acute, lobe sinuses angular; angle between primary lobes 47–75°, incisions

29–57% from lobe apex to midvein; margin serrate; teeth mostly simple, some relatively large, mostly one per secondary, irregularly spaced, distant, apices acute, distal flank concave or straight, proximal flank convex, flexuous, or straight, principal veins present, terminate at apex of tooth; sinus acute; primary venation basal actinodromous; three primary veins, weak, straight, lateral primary veins parallel to divergent from medial secondary veins; basal veins three; secondary venation pinnate within each lobe, craspedodromous and a few camptodromous, spacing irregular; medial secondary pairs ~ six, excurrent attachment, angle of divergence basal 51°, middle 30–35°, apical 30–37°; lobal sinistral bracing formed by bifurcation of a medial secondary vein; tertiary venation reticulate; areoles moderate development, ~4–5 sided.

**Discussion**—We have amended the description provided by Wolfe and Tanai (1987) because they indicated five primary veins in the leaf, but the holotype and paratypes show only three primary veins, and we have included additional specimens. Also, we restrict our concept to the leaves (the holotype is a leaf), whereas the fruits hypothesized by Wolfe and Tanai to have been conspecific are treated here as “*Acer* sp. 2” (See Wolfe and Tanai 1987), Pl. 14, figs. 3, 4). *Acer clarnoense* has shallowly trilobed leaves with some camptodromous external secondary veins (Fig. 4O). It also has acutely angled lobal sinus bracing (Fig. 4P), closely spaced tertiary veins and polygonal areoles with veinlets branching two or three times. The margin is serrate with some of the subsidiary teeth enervated by branches from external secondary veins (rather than directly by the secondary veins) (Wolfe and Tanai 1987, p. 79). This set of features is characteristic of the extant *Macrantha* Pax (1885) group of *Acer* according to Wolfe and Tanai (1987).

ACER CROOKENSE WOLFE & TANAI, 1987

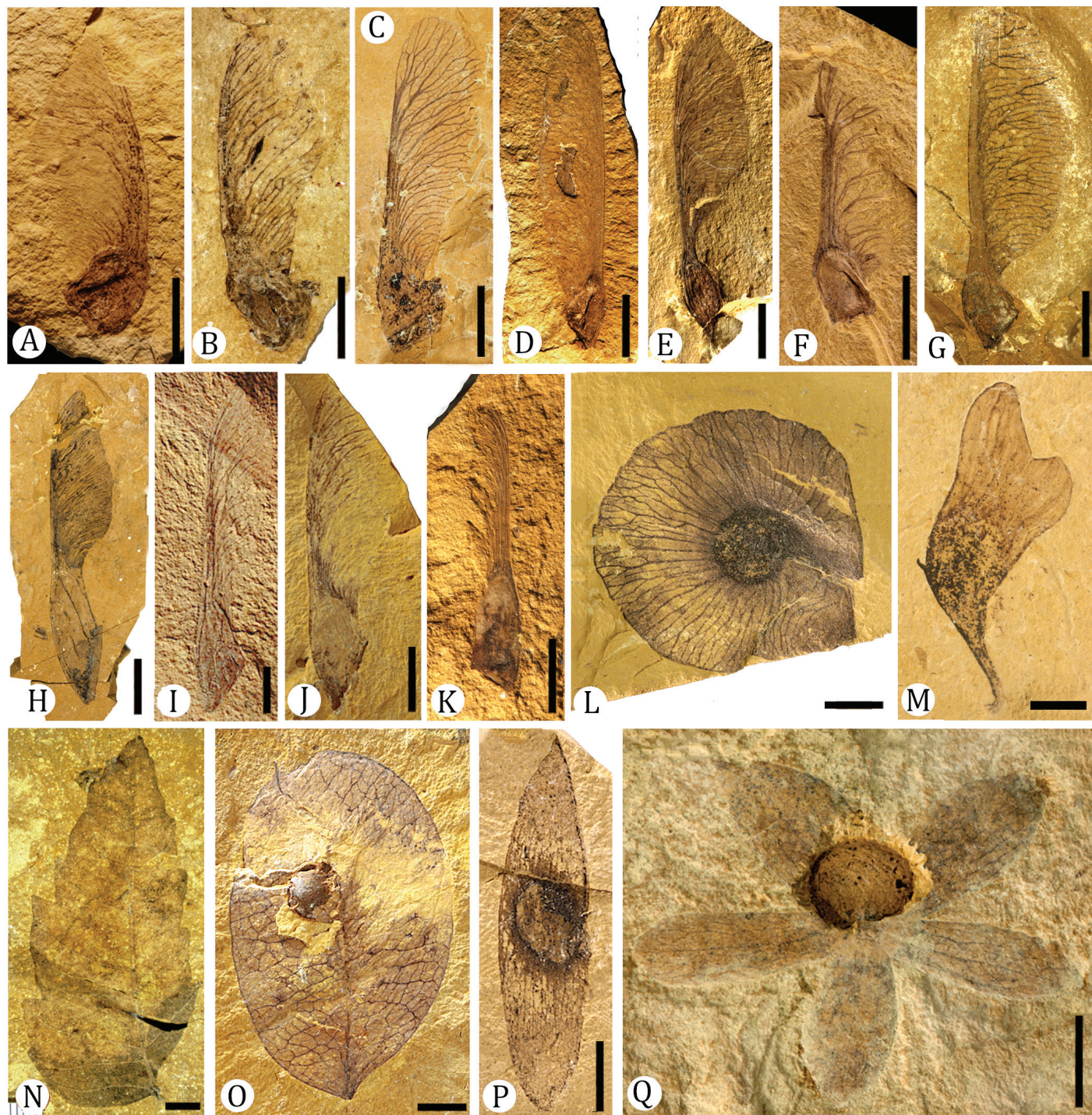
FIG. 5C, D

**Basionym**—*Acer crookense* Wolfe and Tanai, 1987, J. Fac. Sci., Hokkaido Univ. 22, p. 116, pl. 10, figs. 1, 2, 5, 6.

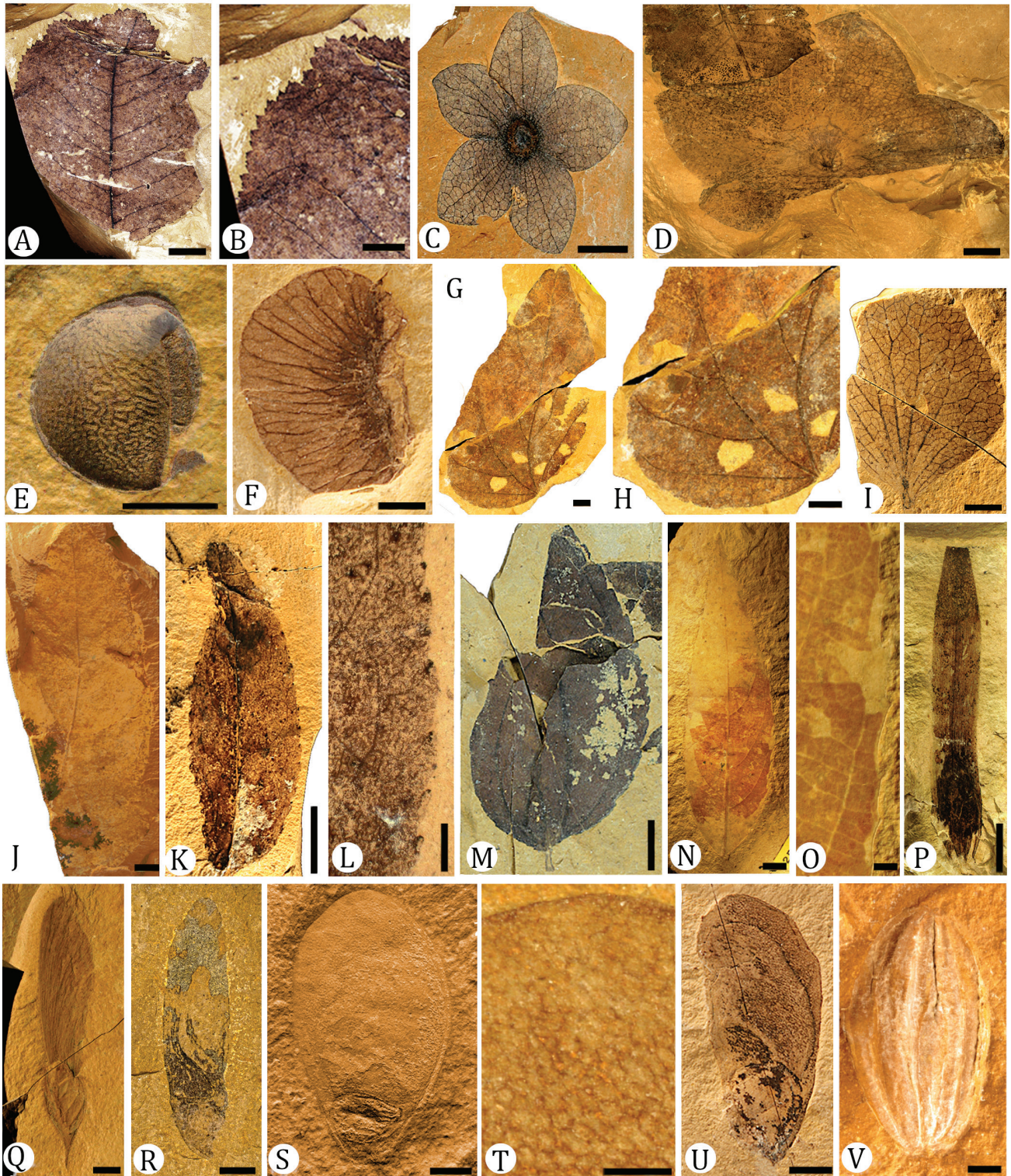
**Holotype**—UCMP 9020A, B.

**Referred specimens**—UF 256-20845, 59035, 59039.

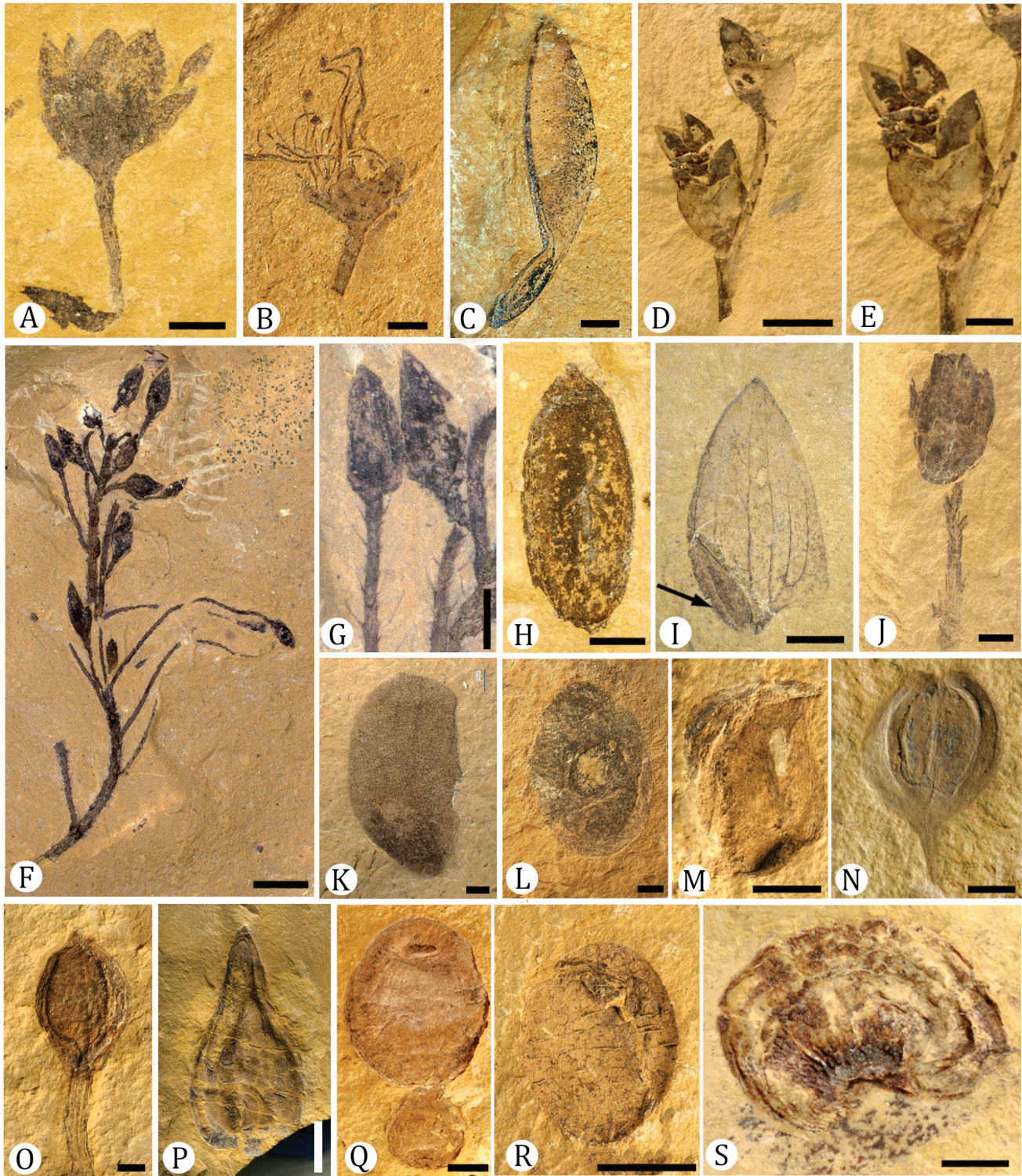
**Description**—Fruit samaroid, with elongate lateral wing in plane of symmetry adjoining a rounded-triangular nutlet; samara length 17–24 mm ( $x=19$ ,  $N=3$ ), width 4.5–5.7 mm ( $x=5.1$ ,  $N=3$ ); apex obtuse-rounded; base truncate; with at least four veins coalesced along straight proximal margin, distal margin shallow convex; wing base forming a wide to narrowly concave sulcus with nutlet; wing vein angle of divergence 11–49°, veins gently



**Figure 5.** Sapindales. **A–K.** *Acer* samaras. **A.** *Acer meyeri* Wolfe and Tanai, Holotype UCMP 9028. **B.** *A. meyeri* (synonym: published as *A. beckii* Wolfe and Tanai, Holotype UCMP 9304. **C.** *A. meyeri*, UF 256-20860. **D.** *A. crookense* Wolfe and Tanai, Holotype UCMP 9020. **E.** *Acer ovipetrinum* Wolfe and Tanai, Holotype, UCMP 9107. **F.** *A. postense* Wolfe and Tanai, UF 256-20841. **G.** *A. postense*, Holotype UCMP 9184. **H.** *Acer sinuofluviatilis* Wolfe and Tanai, Holotype UCMP 9044. **I.** *Acer sinuofluviatilis*, UF 256-20856. **J.** *Acer* sp. 2, UF 256-20857. **K.** *Acer* sp. 2, attributed to *A. clarnoense* by Wolfe and Tanai (1987), UCMP 9014. **L.** *Dipteronia brownii* McClain and Manchester, UF 256-20862. **M.** Morphotype TRR 09, indet. samaroid fruit with stylar projection and distal notch in the wing, UF 256-21012'. **N.** cf. *Elattostachys*, UF 256-21622. **O.** *Koelreuteria allenii* (Lesquereux) Edwards, UF 256-20740. **P.** *Ailanthus confucii* Unger, UF 256-34121. **Q.** *Chaneya tenuis* (Lesquereux) Wang and Manchester, calyx, UF 256-20828. Scale bars: **A–Q**=5 mm; **M**=2 mm.



**Figure 6.** A, B. Morphotype TRL 12, Rosaceae, UF 256-21552. C. *Florissantia ashwillii* Manchester, UF 256-31404. D. *Florissantia speirii* (Lesquereux) Manchester, UF 256-31405a. E. *Rutaspermum* sp., endocarp, lateral view, UF 256-21054. F. *Craigia oregonensis* (Arnold) Kvaček, Bůžek and Manchester, UF 256-20927. G. *Plafkeria* sp., virtually unfolded leaf, UF 256-34107. H. Same, detail of venation. I. *Hydrangea* sp., sepal, UF 256-21005. J. cf. *Ailanthus*, leaflet with rounded teeth, UF 256-21065. K, L. *Flectorivus* sp., UF 256-21424. M. Morphotype TRL 11, cf. Rhamnaceae, UF256-21133a. N, O. Morphotype TRL 13, serrate lamina, UF 256-21545'. P. *Fraxinus* sp., samara, UF 256-20919. Q. *Deviacer wolfei* Manchester, UF 256-20852. R. Morphotype TRR 19, *Cedrela* like seed, UF 256-21049. S, T. Morphotype TRR 04, winged seed, UF 256-21013. U. *Cedrela merrillii* (Chaney) Brown, UF 256-21044. V. *Davidia* sp., endocarp, UF 256-20923. Scale bars: A, C, D, G, H, J, K, M, N, P=5 mm; B=3 mm; E, F, I, Q-S, U, V=2 mm; L, O=1 mm; T=500  $\mu$ m.



**Figure 7.** A. *Antholithes* sp., pedicellate flower, UF 256-20738. B. Morphotype TRR 20, indet. flower, UF 256-21008. C. Morphotype TRR 11, samaroid fruit resembling Fabaceae, UF 256-20921. D, E. Morphotype TRR 07, two sessile infructescences, UF 256-20737a. F, G. Morphotype TRR 12, paniculate infructescence, UF 256-20735. H. Morphotype TRR 13, cf. *Mastixia*, UF 256-20814. I. Morphotype TRR 06, bract with overlapped margin (arrow), UF 256-20928'. J. Morphotype TRR 14, infructescence with overlapping triangular bracts, UF 256-20751. K. Morphotype TRR 05, winged seed, UF 256-20809. L. *Beckersoperma ovalicarpa* (Becker) Meyer and Manchester, winged seed, UF 256-21031. M. Morphotype TRR 15, possible cone scale, UF 256-21574. N. Morphotype TRR 08, pedicellate drupe, UF 256-21010. O. Morphotype TRR 16, pedicellate fruit, UF 256-21009. P. Morphotype TRR 17, pyriform woody structure, UF 256-21016. Q. *Quercus* sp. 3, nut, UF 256-21061. R. Morphotype TRR 10, wide-elliptic fruit, UF 256-21027. S. Morphotype TRR 18, ellipsoidal seed/fruit, UF 256-21052. Scale bars: A, G, H, L, N, O, S=1 mm; B, C, E, F, I, J, M, Q=2 mm; D, P, R=5 mm; K=500  $\mu$ m.

to sharply curving and bifurcating at least three times, numerous anastomosing veins trending perpendicular to distal margin; nutlet length 5.2–6.8 mm ( $x=5.8$ ,  $N=4$ ), width 2.3–4.4 mm ( $x=3.3$ ,  $N=4$ ), apex narrowly rounded, proximal margin straight, distal margin convex or hooked shaped, nutlet with a medial, curved groove, broad at base, narrows upward; attachment scar 2–4 mm, attachment angle 20–59°, nutlet angle 6–19°.

**Discussion**—*Acer crookensis* is distinguished by frequent anastomosing of the venation, and nutlets with a pronounced medial groove. According to Wolfe and Tanai (1987), the nutlet flange (medial groove) observed in these fossils is characteristic of an extinct section of *Acer* they referred to as *Glabroidea*.

*ACER MEYERI* WOLFE & TANAI, 1987

FIG. 5A–C

**Basionym**—*Acer meyeri* Wolfe and Tanai, 1987, J. Fac. Sci., Hokkaido Univ. 22, p. 134, pl. 11, figs. 11, 16

**Synonymy**—*Acer beckii* Wolfe and Tanai, 1987, J. Fac. Sci., Hokkaido Univ. 22, p. 115, pl. 10, figs. 10, 11.

**Holotype**—UCMP 9028.

**Referred specimens**—UCMP 9304 (holotype of *A. beckii*), UF 256-20860, 59034, 59036.

**Description**—Fruit samaroid, with elongate lateral wing in plane of symmetry adjoining an elliptic nutlet; samara length 20–21 mm, width 5–6 mm; apex rounded; base truncate; with at least six veins coalesced along straight proximal margin, distal margin convex; wing base forming a V to U-shaped sulcus with nutlet; wing vein angle of divergence 22–44°, sharply curving and bifurcating up to three times, tending acute or perpendicular to distal margin; nutlet length 6 mm, width 4 mm, apex rounded, proximal and distal margin straight or convex, surface with two distinct flanges, bordering longitudinal furrow that is v-shaped at both ends; attachment angle ~40°, nutlet angle 31°.

**Discussion**—We did not discern significant differences between the holotypes of *A. meyeri* (Fig. 5A) and *A. beckii* (Fig. 5B) as designated by Wolfe and Tanai (1987). Although the former shows venation trending perpendicular to the distal margin and the latter has veins oriented acute to the distal margin, they appear to be identical in nutlet morphology. The nutlet has two distinct flanges that form a V-shaped configuration (Fig. 5A, B) area at the nutlet top, and the proximal margin is markedly convex (Fig. 5A). *Acer meyeri* (including *A. beckii*) conforms to the extinct section of *Acer* named as *Glabroidea* (Wolfe and Tanai 1987).

*ACER OVIPTRINUM* WOLFE & TANAI, 1987

FIG. 5E

**Basionym**—*Acer oviptrinum* Wolfe and Tanai, 1987, J. Fac. Sci., Hokkaido Univ. 22, pgs. 83–84, pl. 20, figs. 4, 6.

**Holotype**—UCMP 9107.

**Discussion**—This species is known only by its holotype although several uncited specimens were mentioned by Wolfe and Tanai (1987). The samara is characterized by a nutlet with a conspicuous basal beak. The nutlet also has eight low ridges and nearly twice the number of thin veins paralleling the ridges. The wing forms a deep and broad U-shaped sulcus with the nutlet, has ten veins coalesced along the proximal margin; wing veins diverge at 10–30° (Fig. 5E). According to Wolfe and Tanai (1987), the elongated nutlet outline, several subparallel nutlet veins, and sinuous proximal margin of the nutlet, are features that link this species with *Acer* section.

*ACER POSTENSE* WOLFE & TANAI, 1987

FIG. 5F, G

**Basionym**—*Acer postense* Wolfe and Tanai, 1987, J. Fac. Sci., Hokkaido Univ. 22, p. 172, pl. 17, figs. 12–14.

**Holotype**—UCMP 9184.

**Referred specimens**—UF 256-20841, 20844, 20848–20850, UCMP 9186, 9230.

**Description**—Fruit samaroid, with elongate lateral wing in plane of symmetry adjoining an elliptic, ovate, or oblate nutlet; samara length 18–22 mm ( $x=20$ ,  $N=5$ ), width 2.7–7.2 mm ( $x=5.3$ ,  $N=5$ ); apex obtuse; base truncate; with 5–6 veins coalesced along nearly straight proximal margin, distal margin deeply convex; wing base extending along apex of nutlet, also forming a U- to V-shaped sulcus with nutlet; wing vein angle of divergence 20–35°, sharply curving and bifurcating 1–3 times, some anastomoses, veinlets reticulate; nutlet length 4.7–7.3 mm ( $x=5.6$ ,  $N=5$ ), width 2.5–5.4 mm ( $x=3.8$ ,  $N=5$ ); apex rounded; proximal margin shallow convex, sometimes expanded beyond proximal margin of wing, distal margin deeply convex; attachment scar 2.5–4 mm; nutlet with some distinct parallel lines at apex, and venation a reticulum; attachment angle 26–80°, nutlet angle 4–17°.

**Discussion**—The original description for *Acer postense* indicates the nutlet shape as elliptic to narrowly ovate, but nutlet shape in UCMP 9230 (Wolfe and Tanai 1987, Pl. 17, fig. 13) is widely ovate. We note a distinctive inverted U-shape to the outline of the nutlet (figs. 5F, G). According to Wolfe and Tanai (1987), *A. postense* conforms to extant *Acer* section *Acer* in having a strongly inflated nutlet with obscurely reticulate venation, and

bifurcating wing veins with reticulate veinlets.

*ACER SINUOFLUVIATILIS* WOLFE & TANAI, 1987

FIG. 5H, I

**Basionym**—*Acer sinuofluviatilis* Wolfe and Tanai, 1987, J. Fac. Sci., Hokkaido Univ. 22, p. 100, pl. 17, figs. 4, 7, 10–12.

**Holotype**—UCMP 9044.

**Referred specimen**—UF 256-20856.

**Description**—Fruit samaroid, with elongate lateral wing in plane of symmetry adjoining an ovate nutlet; samara length 26 mm, width 5.3 mm; apex acute; base truncate; with ~five veins coalesced along straight proximal margin, distal margin broadly convex; wing base extending to ½ distance of nutlet, forming a U-shaped sulcus with nutlet; wing vein angle of divergence 16–22°, veins smooth curving and bifurcating at least two times, some anastomoses; nutlet length 9 mm, width 4 mm, narrowly rounded apex, proximal margin shallow convex, distal margin angular, attachment scar 4.7 mm, nutlet with at least three veins extending from attachment scar apically into the wing, one stronger than others; attachment angle 50°, nutlet angle 10°.

**Discussion**—The presence of veins extending from the attachment scar and entering the wing, where one is stronger than the others (Fig. 5H, 5I), is unique to this species compared to all other *Acer* fruit species in the Teater Road flora. It is similar to *A. cranei* of the Bridge Creek flora and considered likely to belong to *Acer* section *Negundo* (Wolfe and Tanai, 1987).

*ACER* SP. 1 LEAF

FIG. 4Q

**Referred specimen**—UF 256-21128.

**Description**—Lamina ovate, deeply trilobed, small, estimated length 34 mm, estimated width 43 mm, l/w ratio 0.8, leaf area estimate 962 mm<sup>2</sup>, petiole 8 mm long; lamina apex acute; base truncate; one lateral lobe apex acute, lobe sinuses angular, angle between primary lobes 45–74°, incisions around 60% from lobe apex to midvein; margin serrate; teeth simple, sometimes falcate, regularly spaced, distant, apex acute, distal flank concave, straight, or sinuate, proximal flank convex; sinuses angular or rounded; primary venation basal actinodromous; three primary veins, stout, straight, angle of divergence between adjacent primary veins 55°; few secondary veins preserved, craspedodromous, one per tooth; higher order venation not preserved.

**Discussion**—This specimen has characters similar to the *Platanoidea* Group, Section *Manchesteria* Wolfe

and Tanai (1987), with a deeply three lobed leaf, three primary veins, and teeth simple (Fig. 4Q), but the distal flank of the teeth in UF 256-21128 is variable. Specimen UF 256-21388b is a partial lobed leaf with falcate teeth, angular sinus, and sinus angle similar to 21128, but the lobe incision length is unknown. Within this section, *Acer axelrodi* Wolfe and Tanai (1987), from the late middle Eocene of northeastern Nevada, is close to *Acer* sp. 1 but the lack of well-preserved secondaries precludes confirmation (Wolfe and Tanai 1987).

*ACER* SP. 2 FRUIT

FIG. 5J, K

Prior citation. *Acer clarnoense* Wolfe and Tanai, 1987, *pro parte* (fruits only), J. Fac. Sci., Hokkaido Univ. 22, p. 78–79, pl. 14, figs. 3, 4 only.

**Referred specimens**—UF256-20842, 20853, 20854, 20857, 20861, UCMP 9014.

**Description**—Fruit samaroid, with elongate lateral wing in plane of symmetry adjoining an oblong or elliptical nutlet; samara length 16–32 mm ( $\bar{x}$ =24.0, N=7), width 4–11 mm ( $\bar{x}$ =6.0, N=7); apex obtuse; base truncate; with 2–3 veins coalesced along straight proximal margin, distal margin broadly convex or straight, wing base extending to expanded portion of distal margin, forming shallow and broad to rarely deep and short U-shaped sulcus to nutlet; wing vein angle of divergence basal 8–40°, middle 20–40°, apical 16–37°, smoothly to sharply curving and bifurcating 1–3 times, some anastomoses; nutlet length 4–12 mm ( $\bar{x}$ =8, N=8), width 1.4–6 mm ( $\bar{x}$ =4, N=8); narrowly or broadly rounded apex; proximal margin shallow convex, distal margin asymmetrically angular; attachment scar 1–5 mm, sometimes with poorly defined distal keel; nutlet smooth, some with parallel veins running along distal side of nutlet; attachment angle 20–60°, nutlet angle 5–16°.

**Discussion**—*Acer clarnoense* was described on the basis of leaves and fruits but Wolfe and Tanai (1987) selected a leaf as the holotype. Here, we treat the fruits separately as *Acer* sp. 2. These specimens also resemble *A. sinuofluviatilis*, except in that *A. sp. 2* the nutlet surface is smooth and apically rounded (Figs. 5J, K).

*DIPTERONIA* BROWN EMEND. McCLAIN & MANCHESTER, 2001

*DIPTERONIA BROWNII* McCLAIN & MANCHESTER, 2001

FIG. 5L

*Dipteronia brownii* McClain and Manchester, 2001, Am. J. Bot. 88, p. 1320, figs. 10–34.

**Referred specimens**—UF 256-20862, 21046.

**Description**—Fruit a samara, nearly circular, with a

flat scar of detachment from schizocarp; length 11 mm, width ~11 mm; seed nearly circular, length 4.8 mm, width 4.2 mm, centrally positioned within fruit wing, linked with a curved funicle; wing with striations radiating from seed; seed body faintly reticulate.

**Discussion**—As discussed in McClain and Manchester (2001), *Dipteronia brownii* closely resembles extant *D. sinensis* Oliver (1889). *Dipteronia brownii* samaras have also been noted in Sumner Spring, Whitecap Knoll, Ruby Basin, and Florissant floras, and *Dipteronia* sp. in the Bridge Creek flora (Table 2).

*Dipteronia* consists of two species of trees found in temperate forests of China (PoWO 2023). The genus has also been confirmed by fruits from the Late Eocene and Oligocene of China (Manchester 1999, Ding et al. 2018).

CF. *ELATTOSTACHYS* (BLUME) RADLKOEFER, 1879

FIG. 5N

**Referred specimens**—UF 256-21539, 21622, 21648, 78833.

**Description**—Lamina ovate, asymmetrical, unlobed, small or notophyll, length 58–104 mm ( $x=81$ ,  $N=2$ ), width 25–47 mm ( $x=33$ ,  $N=4$ ), l/w ratio 2.2–2.3, leaf area estimate 967–3269 mm<sup>2</sup> ( $x=2118$ ,  $N=2$ ), petiole missing; lamina apex acute; base rounded and highly asymmetrical; margin serrate; teeth simple, one order of large to small teeth, irregular, distant, apices acute; teeth distal flank straight and slightly sinuous, proximal flank convex to straight, tooth apex rounded to sometimes acute; sinuses angular; venation pinnate; midvein moderately thick, straight; secondary venation with alternate pairs of craspedodromous secondaries, other pairs brochidodromous, 14 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 53–88°, middle 64–90°, apical 54–71°, course curved and sinuous; brochidodromous secondaries with exmedial tertiary vein to sinus; intersecondaries frequent, extending up to ½ distance to margin before merging with tertiaries; tertiary venation sparsely percurrent; quaternary venation reticulate.

**Discussion**—These leaflets resemble those assigned to *Dipteronia insignis* (Lesquereux) Brown (1937) from the Florissant, Beaverhead Basins, and Metzel Ranch floras (MacGinitie 1953, Becker 1969, 1972). As noted in McClain and Manchester (2001), the systematic affinity of this foliage remains elusive because similar kinds of leaflets can be found in various genera of Sapindales, such as *Koelreuteria* and *Dipteronia*. Given that the Teater Road flora includes verified fruits of both *Dipteronia* and *Koelreuteria* we considered both of these genera as potential candidates for the identity of this foliage. In

the extant species, *Koelreuteria elegans* (Seemann) A.C. Smith (1952), the leaflets have predominantly simple teeth whereas *K. paniculata* Laxmann (1772) leaflets have predominantly compound teeth. In *K. elegans*, the secondary veins are predominantly cladodromous-like with the veins bifurcating near the margin, with one branch extending to the tooth, and the other to the sinus, while in *K. paniculata* the secondaries are craspedodromous, lacking brochidodromous venation. In *Dipteronia sinensis* Oliv. (1889), the percurrent tertiary veins along the margin merge with the sinus, while in *D. dyeriana* A. Henry (1903), exmedial branches of the craspedodromous secondaries enter the tooth and/or sinus. Extant *Elattostachys verrucosa* (Blume) Radlkofer (1933) (Sapindaceae) shows numerous morphological similarities to our fossil specimens, such as asymmetrical leaf and base, simple, one order of large to small teeth, craspedodromous alternating with brochidodromous secondaries, percurrent tertiaries; reticulate quaternaries, and frequent intersecondary veins. However, in *E. verrucosa* there are semicraspedodromous mixed with craspedodromous secondaries and the teeth are occasionally compound. We tentatively place these specimens near *Elattostachys*.

*Elattostachys* consists of 14–20 species of trees found in Malaysia to Australia, and Polynesia (Delaude 1993, GBIF 2021, PoWO 2023).

*KOELREUTERIA* LAXMANN, 1772

*KOELREUTERIA ALLENII* (LESQUEREUX) EDWARDS, 1927

FIG. 5O

*Koelreuteria allenii* (Lesquereux) Edwards, 1927, *J. Nat. Hist.* 20, p. 109–110.

**Referred specimens**—UF 256-20739–20748a, 21015, 34097, 34098.

**Description**—Fruit with elliptic capsular valves; length 24–37 mm ( $x=32$ ,  $N=8$ ), width 13–24 mm ( $x=19$ ,  $N=9$ ); apex mucronate; base narrowly cuneate, usually symmetrical (one specimen asymmetrical); margin entire; valves with sinuous lateral veins, extending to fimbrial vein at the margin, veins branched, connected into quadrilateral to pentagonal areoles that are irregular and elongate, transverse to longitudinal freely ending veinlets unbranched to once branched; seeds ellipsoidal, attached to the midvein, midway between base and apex of valve; seed diameter 2.0–5.4 mm, smooth to faintly ridged; septa extend approximately 1/3 to 2/3 of valve length; valve texture membranous.

**Discussion**—Characters that place these fruits in Sapindaceae, specifically *Koelreuteria*, are elliptic

membranous valves greater than 20 mm long, with an elongated reticulum (Fig. 5O). An incomplete septum extending about halfway from base toward the apex of the valve, with two seeds at a single level within each valve is another important character, but only one seed per specimen is preserved (Wang et al. 2013). Along with the aforementioned characters, a cuneate base places these specimens into *Koelreuteria allenii* which is also found in the Florissant and Green River floras. Other *Koelreuteria* species with fruits have been recognized in the Mormon Creek, Metzel Ranch, Ruby Basin and Beaverhead Basins floras (Table 2, Wang et al. 2013).

*Koelreuteria* consists of 3–4 species of trees, found in temperate forests of China, North Vietnam and Lorea, Taiwan and Fiji (Wang et al. 2013, PoWO 2023).

SIMAROUACEAE DE CANDOLLE, 1811  
*AILANTHUS* DESFONTAINES, 1788  
*AILANTHUS CONFUCII* UNGER, 1850

FIG. 5P

*Ailanthus confucii* Unger, 1850, Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 2.

**Referred specimens**—UF 256-20701, 20703a-20708, 20710a-20712, 20715-20718, 20720-20722, 20724a-20733, 20736, 20820, 21143b, 21584, 21586, 34112, 34119-34121, 47239, 60441, 60442, 60445-60448, 76956.

**Description**—Samaroid mericarp, with a centrally placed oval to rounded seed surrounded by a narrowly elliptic wing that tapers to both ends; mericarp length 12–36 mm ( $x=24$ ,  $N=30$ ), width 4.3–11 mm ( $x=6$ ,  $N=40$ ); attachment end acute, apical end rounded and sometimes twisted; ventral margin sometimes forms a v-shape above the seed; venation of ~15 parallel veins that radiate from a reticulum over the seed body and extend out to the ends of the samara; a strong ventral vein arising from the attachment end extends along the margin to near the fruit midsection, then arches inward to the seed; seed body length 3.7–7 mm ( $x=5$ ,  $N=36$ ), width 2.8–6 mm ( $x=4$ ,  $N=37$ ).

**Discussion**—These specimens conform to *Ailanthus*, characterized by shape, size, venation pattern, and seed placement (Fig. 5P). The fossil record of *Ailanthus* is easily recognized on the basis of such distinctive winged fruits. Due to morphological homogeneity of fossil fruits found in Europe, North America, and Asia, nearly all have been synonymized under the name of *Ailanthus confucii* (Corbett and Manchester 2004). The Teater Road fruits

were mentioned and figured previously as *Ailanthus* sp. in Manchester (1999, Fig. 13B)) and Corbett and Manchester (2004, see Fig. 5L and 5M). *Ailanthus* fruits are also found in Green River, Sumner Springs, Whitecap Knoll, Florissant, Metzel Ranch, Ruby and Beaverhead Basins floras (Table 2).

*Ailanthus* consists of 5–6 species of trees, found in tropical and subtropical regions of Asia to Northern Australia, and naturalized in North America, Central and Southern Europe (Mabberley 1993, Corbett and Manchester 2004, GBIF 2021, PoWO 2023).

CF. *AILANTHUS*

FIG. 6J

**Referred specimens**—UF 256-21065, 21234, 34073.

**Description**—Lamina ovate to lanceolate, symmetrical, unlobed, small, length 63–71 mm ( $x=68$ ,  $N=3$ ), width 22–29 mm ( $x=26$ ,  $N=3$ ), l/w ratio 2.5–2.9, leaf area estimate 911–1329 mm<sup>2</sup> ( $x=1179$ ,  $N=3$ ), petiolule missing; lamina apex acute; base cuneate; margin mostly entire, with single large tooth at base of lamina and 1–2 smaller irregularly spaced teeth below midsection of lamina, apex rounded; venation pinnate; midvein weak or moderate, curved; secondary venation rarely craspedodromous, mostly brochidodromous, ~eight pairs, spacing irregular, excurrent or decurrent attachment, angle of divergence 40–70°, course straight to arching upward; 1–2 secondaries extending  $\geq \frac{1}{2}$  distance to margin then merging with tertiary veins; tertiary venation reticulate; quaternary venation reticulate.

**Discussion**—For an example of an extant species similar to our specimens, we selected *Ailanthus altissimus* (Miller) Swingle (1916), characterized by one or a few large teeth near the base of the lamina, and few irregular spaced teeth below midsection of lamina (Fig. 6J). However, the Teater Road specimens lack prominent circular glands at the teeth apices as in *A. latissimus* and *A. excelsus* Roxburgh (1795) (Corbett and Manchester 2004, see Figs. 3C, D, G, H). We are uncertain whether the lack of glandular tips on the teeth is a preservational difference or a fundamental distinction that would preclude placement of these specimens in *Ailanthus*.

MALVALES JUSSIEU EX BERCHTOLD &amp; J. PRESL, 1820

MALVACEAE JUSSIEU, 1789

*CRAIGIA* W.W. SMITH & W.E. EVANS, 1921*CRAIGIA OREGONENSIS* (ARNOLD) KVAČEK, BŮŽEK, MANCHESTER, 1991

FIG. 6F

*Craigia oregonensis* (Arnold) Kvaček, Bůžek, Manchester,

1991, Bot. Gaz. 152, p. 522.

*Koelreuteria oregonensis* Arnold, 1952, The Paleobotanist 1, p. 77, figs. 1–3.

**Referred specimens**—UF 256-21001, 21003, 20863, 20927.

**Description**—Membranous fruit valves, half-elliptical with a straight proximal margin of detachment and convex distal margin, length 10–12 mm ( $x=10.4$ ,  $N=2$ ), est. width 12–16 mm ( $x=14$ ,  $N=3$ ); secondary veins radiating from edge of the septum, which is about 2 mm thick, veins mostly straight; secondary and tertiary veins dichotomizing and anastomosing, ultimately joining into a fimbrial vein; areoles elongate.

**Discussion**—Only partial fruit valves are present (Fig. 6F) but they are very similar, morphologically, to those of *Craigia oregonensis* from the Bridge Creek flora (Table 2, Meyer and Manchester 1997). The few specimens from Teater Road are, however, significantly smaller than those from the Bridge Creek flora (10–12 vs 18–30 mm long) *Craigia* fruits have also been found in Whitecap Knoll, Mormon Creek, Ruby Basin, Beaverhead Basins and Green River floras (Table 2). The extensive fossil record of this genus in western North America, Europe and Asia, was reviewed by Kvaček et al. (2005).

*Craigia* consists of two extant species of trees, found primarily in wet tropical biomes of Tibet, Southern China to Vietnam (Kvaček et al. 2005, Ding et al. 2019, GBIF 2021, PoWO 2023).

*PLAFKERIA* WOLFE, 1977

*PLAFKERIA* sp.

FIG. 6G, H

**Referred specimens**—UF 256-21126, 21630, 21650, 34107.

**Description**—Lamina ovate or widely ovate, asymmetrical, small or notophyll, length 25–80 mm ( $x=53$ ,  $N=2$ ), width 22–61 mm ( $x=42$ ,  $N=3$ ), l/w ratio 1.2–1.7, leaf area estimate 364–2376 mm<sup>2</sup> ( $x=1370$ ,  $N=2$ ), petiole missing; lamina apex acute; base asymmetrical, obtuse or acute; margin entire, undulate basally; primary venation basal actinodromous; simple agrophic veins; secondary venation pinnate, brochidodromous, ~four pairs, spacing irregular, excurrent attachment, angle of divergence 17–55°; tertiary veins opposite percurrent; epimedial tertiaries opposite percurrent, proximal course perpendicular to midvein, distal course basiflex; higher order veins orthogonal reticulate.

**Discussion**—These specimens are similar to *Plafkeria obliquifolia* (Chaney) Wolfe (1977) from Bridge Creek and Badger's Nose flora (Meyer and Manchester 1997,

Myers 2006) but because the petiole is not preserved in the Teater Road specimens, we cannot confirm that it was inflated as in *P. obliquifolia*. Aside from Teater Road and Bridge Creek floras, *Plafkeria* has not been observed in our selected sites of western United States (Table 2). *Plafkeria* is a fossil genus that accommodates leaves with characters found in more than one modern genus of Malvaceae (which includes former Sterculiaceae and Tiliaceae, Soltis et al. 2018) such as *Burretiodendron* Rehder (1936), *Tilia* L. (1753), and *Pterospermum* Schreber (1791), and to a lesser extent the cornalean genus *Alangium* Lamarck (1783) (Alangiaceae) due to the configuration of quaternary and higher order venation (Meyer and Manchester 1997).

*FLORISSANTIA* KNOWLTON EMEND. MANCHESTER, 1992

*FLORISSANTIA* ASHWILLII MANCHESTER, 1992

FIG. 6C

*Florissantia ashwillii* Manchester, 1992, Am. J. Bot. 79, p. 1005, figs. 33–42, 48–50.

**Holotype**—UF 256-11740 (figs. 35, 48–50 in Manchester 1992)

**Referred specimens**—UF 256-11739, 11741, 11742, 11749, 20865, 20866a, b, 20868–20874, 20876–20883, 20885–20893, 20895, 20897–20899, 20902, 20903, 21473b, 31404, 34068, 34076, 34117, 78150, 78829, 78830.

**Description**—Fruits with calyx diameter 9–31 mm ( $x=20$ ,  $N=39$ ), gamosepalous, deeply campanulate, five-parted; sepals acute to rounded, with radiating primary venation; calyx incision 28–40%, each sepal has 3–5 primary veins diverging from pedicel scar and extending in a straight to slightly sinuous course to near margin, sometimes dividing near upper margin, then looping to join adjacent primary vein; fruit body rounded pentagonal, sepals with three primary veins and usually two strong veins that extend ½ sepal length; basal prominent vein of sepal branches to form sinal bracing; primary veins joined by secondary reticulate veins; androgynophore forming a circular disk.

**Discussion**—The extinct genus *Florissantia* (Malvaceae) is recognized by its campanulate, five-lobed persistent calyx (Fig. 6C), accompanied by a pentacarpellate gynoecium and ten stamens (Manchester 1992, Meyer and Manchester 1997). Two species of *Florissantia* are recognized in the Teater Road assemblage; *Florissantia ashwillii* (Manchester 1992) is the more abundant one at this site. It has relatively small calyces. Some of the Teater Road specimens preserve stamens that yielded well-preserved pollen with features distinctive of tilioid

Malvaceae (Figs. 48 to 50 in [Manchester 1992](#)). This species is also found in Sumner Spring and Whitecap Knoll floras (Table 2).

*FLORISSANTIA SPEIRII* (LESQUEREUX) [MANCHESTER, 1992](#)  
FIG. 6D

*Florissantia speirii* (Lesquereux) [Manchester, 1992](#), *Am. J. Bot.* 79, p. 1003–1004, figs. 1–22.

*Porana speirii* [Lesquereux, 1883](#), *Rept. U.S. Geol. Surv. Terr.* 8, p. 172, pl. 28, fig. 15.

**Referred specimens**—UF 256-20884, 31405a.

**Description**—Fruit incomplete; calyx estimated diameter 26–39 mm ( $x=33$ ,  $N=2$ ), gamosepalous, shallowly campanulate; apparently five-parted; calyx lobes rounded, with primary radiating venation; calyx incision 15%; each sepal has 5–6 primary veins diverging from base and extending in a straight course to near the margin then looping to join adjacent primary vein; exmedial branching of primary vein leading to sinuses forming sinular bracing; primary veins joined by secondary reticulate veins.

**Discussion**—These specimens are distinguished from the aforementioned species by the larger calyx size and shallower sinuses of the calyx (Fig. 6D). They resemble those known from more complete specimens, including some with intact stamens and in situ pollen from the Bridge Creek and Florissant floras ([Manchester 1992](#)). The lack of a whorl of small petals distinguishes these specimens from *Florissantia quilchenensis* (Mathewes and Brooke) [Manchester \(1992\)](#) found in the Eocene of British Columbia and northeastern Washington. *Florissantia speirii* is also found in the Florissant, Ruby Basin, Beaverhead Basins, and the Clarno West Branch Creek floras, and extends to the Oligocene Bridge Creek flora (Table 2).

CORNALES [LINK, 1829](#)  
HYDRANGEACEAE [DUMORTIER, 1829](#)  
*HYDRANGEA* [LINNAEUS, 1753](#)  
*HYDRANGEA* SP.

FIG. 6I

**Referred specimens**—UF 256-21005–21007.

**Description**—Sepal; obovate, asymmetrical or symmetrical, length 11–15 mm ( $x=13$ ,  $N=3$ ), width 10–16 mm ( $x=13$ ,  $N=3$ ); apex rounded, obtuse; base obtuse or acute with pointed attachment scar; margin entire; primary venation actinodromous; secondary and tertiary venation reticulate and forming two or more rows of marginal loop; fimbrial vein lacking.

**Discussion**—These isolated sepals (Fig. 6I) correspond

in shape, size, and venation to those found intact in complete calyces of four (occasionally three-) sepals at other Eocene to Miocene sites. Unlike *Florissantia*, these sepals are completely free from one another rather than connate. These sepals resemble those of extant species of *Hydrangea* with palmately veined calyces and resemble the figures of *Hydrangea florissantia* Cockerell (1908) ([MacGinitie 1953](#)) from Florissant, *H. knowltonii* [Manchester \(2015\)](#) from the Clarno Formation ([Manchester et al. 2015](#)), and *Hydrangea* sp. from the Bridge Creek flora (Table 2, [Meyer and Manchester 1997](#)). As noted in [Meyer and Manchester \(1997\)](#), it is difficult to distinguish extant species of *Hydrangea* based only on calyx morphology, hence we do not provide a specific assignment for the Teater Road specimens. *Hydrangea* fruits and calyces are also found at sites of Clarno Formation, and in Whitecap Knoll, Mormon Creek and Beaverhead Basins, and Bridge Creek floras (Table 2), and were recognized from the Eocene Chuckanut Formation of Washington ([Mustoe 2002](#)).

*Hydrangea* consists of 23–80 extant species of shrubs and occasional lianas, found in Eastern Asia to New Guinea, Eastern United States to northwestern South America, southern South America, Kuri and Hawaiian Islands ([Mabberley 1993](#), [GBIF 2021](#), [PoWO 2023](#)).

NYSSACEAE [JUSSIEU EX DUMORTIER, 1829](#)  
*DAVIDIA* [BAILLON, 1871](#)  
*DAVIDIA* SP.  
FIG. 6V

**Referred specimen**—UF 256-20923.

**Description**—Fruit stone elliptic; length 15 mm, width 9 mm, with multiple longitudinal ribs, a thinner rib between each pair of thicker ribs.

**Discussion**—An elliptic fruit with a thinner rib between each pair of thicker ribs (Fig. 6V) is similar to extant *Davidia involucrata* Baillon (1871), except fruits of the latter are nearly twice as large. Well preserved silicified fruits of similar size and external morphology were confirmed as *Davidia* by their internal morphology from the nearby Dietz locality, UF 279 (figs. 65–69 in [Manchester and McIntosh 2007](#)). A fruit with possible thick ribs is indicated as cf. *Nyssa* L. (1753) in the Beaverhead Basins flora (pl. 42, fig. 15a in [Becker 1969](#)).

*Davidia* consists of one extant species of tree endemic to central China ([Ying et al. 1993](#), [Manchester et al. 2009](#), [PoWO 2023](#)).

ERICALES [BERCHTOLD & J. PRESL, 1820](#)  
STYRACACEAE [DE CANDOLLE & SPRENGEL, 1821](#)  
*FLECTORIVUS* [MEYER & MANCHESTER, 1997](#)

*FLECTORIVUS* SP.

FIG. 6K, L

**Referred specimens**—UF 256-21375, 21424, 21550, 21654.

**Description**—Lamina elliptic or narrowly elliptic, asymmetrical, unlobed, nanophyll or small, length 22–39 mm ( $x=29$ ,  $N=3$ ), width 9–32 mm ( $x=16$ ,  $N=4$ ), l/w ratio 1.5–3.8, leaf area estimate 148–273 mm<sup>2</sup> ( $x=214.0$ ,  $N=3$ ), petiole missing; lamina slightly rounded; base cuneate and asymmetrical; margin serrate; teeth simple, with small, regularly spaced, distant, glandular teeth, with rounded or acute apices; venation pinnate; midvein stout, slightly curved; secondary venation semicraspedodromous, ~eight pairs, irregular spacing, excurrent attachment, angle of divergence basal and middle 48–90°, apical 38–57°, course slightly sinuous to ½ distance to margin, then arching apically and parallel with margin; intersecondaries less than one per intercostal; tertiaries reticulate; marginal tertiaries forming a uniseriate series of exmedial brochidodromous loops, giving rise to tertiary branches that enter the teeth; higher order venation indiscernible.

**Discussion**—*Flectorivus* is an extinct genus possessing foliage similar to extant *Styrax* L. (1753), *Melliodendron* Handel-Mazzetti (1922) and *Pterostyrax* Siebold and Zuccarini (1839) (Styracaceae, Meyer and Manchester 1997). For an example of an extant species that is similar to our specimens, we selected *Styrax americanus* Lamarck (1783), with characters of marginal tertiaries forming a uniseriate series of exmedial brochidodromous loops, and tertiary branches from these exmedial loops terminating in small apically oriented glandular teeth (Fig. 6K). The venation entering the teeth of *S. americanus* is complex, with tertiary veins originating from tertiary vein looping, and minor secondary veins originating from secondary vein looping. These specimens are also similar to *Flectorivus microdontos* Meyer and Manchester (1997) from Bridge Creek (Table 2) and Badger's Nose floras (Meyer and Manchester 1997, Myers 2006) with small glandular teeth close into the margin (Fig. 6L) but *F. microdontos* is nearly 2.5x larger than our specimens, and higher order venation is not sufficiently well-preserved in our specimens for specific assignment. *Styrax transversa* MacGinitie (1969) from the Green River flora is distinguished from the Teater Road material by its acuminate apex and craspedodromous secondary venation (MacGinitie 1969). Both *S. curvatus* Potbury (1935) from the Late Eocene La Porte flora of California and *S. laramiensis* Lesquereux (1888)

from the Denver flora have entire margins (Lesquereux 1888, Potbury 1935). *Styrax crenatus* MacGinitie (1937) from the Miocene Weaverville flora of California seems to be similar in margin, secondary venation and marginal tertiary venation, but the intercostal venation is not well-preserved in the Teater Road specimens for confirmation (MacGinitie 1937). Specimen UF 256-34109 has apically directed glandular teeth preserved only in the apical section, while tertiary venation is percurrent.

GARRIALES LINDLEY, 1846

EUCOMMIACEAE ENGLER, 1907

*EUCOMMIA* OLIVER, 1890*EUCOMMIA MONTANA* BROWN, 1940

FIG. 1L

*Eucommia montana* Brown, 1940, J. Wash. Acad. Sci. 30, p. 349–350, fig. 3.

**Referred Specimens**—UF 256-11051, 20813, 20927, 34102.

**Description**—Samaras obovate or elliptic; stipitate, length 8–11 mm ( $x=9$ ,  $N=3$ ), width 4.4–5.7 mm ( $x=5.2$ ,  $N=3$ ); apex acute, stigmatic cleft subapical; base acute; seed body elliptic, surface reticulate, length 3.5–6 mm ( $x=5$ ,  $N=3$ ), width 1.7–2.5 mm ( $x=2.2$ ,  $N=3$ ).

**Discussion**—A more complete description and discussion of the distinctive fossil fruits of *Eucommia montana* can be found in Call and Dilcher (1997). *Eucommia montana* also occurs at the Metzel Ranch (Becker, 1972) and Whitecap Knoll floras (Manchester, 2000). Fruits of the genus are also known from the Sumner Spring, Ruby Basin and Florissant floras (Table 2).

*Eucommia* consists of one extant species of tree, found in mixed mesophytic forests of China (Mabberley 1993, Call and Dilcher 1997, PoWO 2023), but during the Cenozoic it was distributed in North America as far south as southern Mexico, and in Europe and Asia (reviewed in Manchester et al. 2009).

LAMIALES BROMHEAD, 1838

OLEACEAE HOFFMANNSEGG &amp; LINK, 1809

*FRAXINUS* LINNAEUS, 1753*FRAXINUS* SP.

FIG. 6P

**Referred specimens**—UF 256-20919, 20920, 78831.

**Description**—Fruit with a thin, short pedicel; samaroid, bilaterally symmetrical, with elongate lateral wing in plane of symmetry adjoining a seed; fruit length 16–24 mm ( $x=20$ ,  $N=2$ ), width 1.3–2.9 mm ( $x=2.1$ ,  $N=3$ ); apex and base acute; peduncle length 0.7 mm; margins straight; wing ensiform, length 12–24 mm ( $x=18$ ,  $N=2$ ),

width 1.3–2.2 mm ( $x=1.8$ ,  $N=2$ ); venation consisting of numerous fine, parallel veins, and presence of a midvein, extending from seed to wing apex; wing base extending down lateral margin to  $\frac{1}{2}$  seed length; seed body elliptic, length 4.2–11 mm ( $x=6$ ,  $N=3$ ), width 1.9–4.8 mm ( $x=3.1$ ,  $N=3$ ).

**Discussion**—These specimens (Fig. 6P) conform to extant *Fraxinus*, the samaras of which are found in the Eocene to Miocene floras of North America, Oligocene to Pliocene floras of Europe, and Miocene to Pliocene floras of Asia (Call and Dilcher 1992, Manchester 1999, Mathewes et al. 2021). *Fraxinus* fruits are also confirmed from Mormon Creek, Metzler Ranch, Ruby, Beaverhead Basins and Bridge Creek floras (Table 2).

*Fraxinus* consists of 58–65 species of trees, found in North and Central America, Cuba, temperate Eurasia to Central and Southern Malesia (Macoboy 1991, Maberley 1993, GBIF 2021, PoWO 2023).

INCERTAE SEDIS

ANGIOSPERMAE LINDLEY, 1830

DEVIACER MANCHESTER EMEND. MYERS & ERWIN, 2015

DEVIACER WOLFEI MANCHESTER, 1994

FIG. 6Q

*Deviacer wolfei* Manchester, 1994, *Palaeontogr. Am.* 58, p. 85, pl. 39, figs. 1–6, text-figure 17B.

**Referred specimens**—UF 256-20852, 20858, 34124, 87100.

**Description**—Fruit samaroid, with elongate lateral wing in plane of symmetry adjoining an elliptical nutlet; wing length 16–18 mm, width 4–7 mm; wing dorsal margin straight to slightly convex, rounded apically, ventral margin straight or concave basally forming a sulcus adjacent to the nutlet, convex, deep to shallow rounded apically; venation parallel, dichotomizing, running parallel to dorsal margin in increasing apical distance from ventral to dorsal margins, then arching towards ventral margin, veins closer together along dorsal margin of wing; nutlet length 4–7 mm, width 1.5–3.5 mm; rounded apically with a flat edge on dorsal margin; attachment angle 30–46°, nutlet angle 6–17°.

**Discussion**—*Deviacer* can be distinguished from *Acer* by the lack of a ventral attachment scar on the nutlet (Manchester 1994). Although the relatively flat margin on the dorsal margin of the nutlet was originally interpreted as a scar from schizocarpic detachment, we have not seen sufficient evidence to indicate these were not solitary fruits. Aside from Teater Road, this species has not been noted within our selected sites of western United States but is common in the Middle Eocene Clarno localities of

Oregon (Table 2, Manchester 1994). The familial affinity of *Deviacer* remains, in our opinion, uncertain.

MORPHOTYPE TRL 10

FIG. 2I, J

**Referred specimen**—UF 256-21387.

**Description**—Lamina elliptic, symmetrical, unlobed, small, estimated length 41 mm, width 13 mm, l/w ratio 3.2, leaf area estimate 349 mm<sup>2</sup>, petiole length 2 mm; lamina apex missing; base cuneate; margin entire; venation pinnate; midvein stout, straight; secondary venation brochidodromous, ~11 pairs, irregularly spaced, excurrent attachment, angle of divergence basal 33–42°, middle 32–47°, apical 51–53°, course straight to curved and slightly sinuous; secondaries occasionally divide ~ $\frac{1}{2}$  distance to margin before joining adjacent secondaries; usually one intersecondary per intercosta, extending >  $\frac{1}{2}$  to margin before splitting and joining both super and subadjacent secondaries, or curving upward to join with superadjacent secondaries; tertiary and quaternary veins irregularly reticulate, forming quadrangular to pentagonal cells; free ending veinlets mostly one branched; occasional circular structures at confluence of tertiary veins.

**Discussion**—This entire-margined leaf with brochidodromous secondary veins, irregularly reticulate tertiary and quaternary veins and free ending ultimate veins (Fig. 2I) is unique among the morphotypes from this flora. However, this set of characters is found in extant Fabaceae, Magnoliales Bromhead (1838), Laurales, Fagaceae, and many other angiosperm taxa. The lack of cuticular characters make it almost impossible to identify this specimen even to a family level. Our fossil specimen is similar to entire-margined leaves of *Lithocarpus coatsii* Axelrod (1966) from the Eocene of Nevada (Axelrod 1966), but *L. coatsii* is in need of re-examination according to Manchester and Crane (1983).

PROTEALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820

CF. PROTEACEAE JUSSIEU, 1789

MORPHOTYPE TRR 04

FIG. 6S, T

**Referred specimen**—UF 256-21013.

**Description**—Seed winged; elliptic, length 14 mm, width 8 mm; one wing extending laterally from seed body; apex obtuse; base acute; proximal and distal shallow convex; wing base extend along seed body apex; wing with vein along both proximal and distal margins, extending to  $\frac{1}{2}$  wing length, vein thick when emerging from seed body apex; wing surface pattern of distinct round cells; seed body obovate, length 3.6 mm, width

3.6 mm, in-line with wing mid-line.

**Discussion**—We conducted a survey of numerous extant angiosperm winged seeds with a similar overall shape, having an elliptical seed body at one end and a single elongate wing that lacks prominent venation (Fig. 6S) (Lott and Manchester, unpublished data). This specimen conforms to extant *Lomatia* R. Brown (1810), characterized by an elliptic, single winged seed, with a vein running alongside the margins, thicker near seed body apex proximally, wing surface with evident cellular pattern (Fig. 6T), and obovate seed body. However, in *Lomatia* the vein extends along the entire margin, and the wing cells are pentagonal and oblong. This specimen is only tentatively placed in Proteaceae because we have only one specimen, and if so, is unique in the Eocene/Late Oligocene of western North America. *Lomatia lineata* (Lesquereux) MacGinitie (1953) leaves were recognized at Florissant, Green River and Ruby Basin floras (MacGinitie 1953, Becker 1961) but its validity since been in question because the fruits that MacGinitie considered to be conspecific were subsequently found attached to a branch with ulmaceous leaves, now considered as *Cedrelospermum* (Manchester 1989b).

*Lomatia* consists of 11–12 species of shrubs or trees found in Australia and South America (Mabberley 1993, GBIF 2021).

ROSALES BERCHTOLD & J. PRESL, 1820  
CF. RHAMNACEAE JUSSIEU, 1789  
MORPHOTYPE TRL 11

FIG. 6M

**Referred specimen**—UF256-21133a.

**Description**—Lamina ovate, symmetrical, unlobed, nanophyll, estimated length 34 mm, width 16 mm, l/w ratio 2.1, leaf area estimate 371 mm<sup>2</sup>, petiole length 2 mm; lamina apex missing; base rounded; margin serrate, teeth compound, with two orders of teeth, 1–2 inconspicuous teeth on proximal flank of primary tooth, usually regularly spaced, distant, apex rounded or acute, distal flank straight to concave, proximal flank broadly convex; sinuses angular to rounded; primary venation basal acrodromous, one pair of strong lateral primaries, curving upward toward middle of leaf; one pair of basal secondary veins, exmedial of lateral primary veins, running close to leaf margin and curving upward toward leaf apex; higher order venation not preserved.

**Discussion**—The presence of actinodromous venation with two strong lateral primaries arching towards the leaf apex, and serrate margin are features common in Rhamnaceae (Meyer and Manchester 1997), and is

consistent with *Paliurus* foliage, a genus which is confirmed from fruits at Teater Road, but our assignment is tentative due to poor preservation of secondary and tertiary venation (Fig. 6M). The presence of three acrodromous primaries and one pair of basal secondary veins arching towards the leaf apex can be found in extant *Ziziphus inerma* Merrill (1905) where the basal secondaries are slightly wavy, and *Talguenea quinque-nervia* (Gillies and Hooker) I.M. Johnston (1929) where one secondary vein extends to the apex or the pair of secondaries extend to near ½ leaf length, although both species have entire margins. This specimen is similar in shape, venation, and margin to the fossil species *Paliurus blakei* (Chaney) Meyer and Manchester (1997) from the Bridge Creek flora (Meyer and Manchester 1997). Unfortunately, morphological features of *Paliurus* and *Ziziphus* leaves can be indistinguishable. *Ziziphus florissantii* (Lesquereux) MacGinitie (1953) is found in the Florissant flora, and a small Rhamnaceae leaf occurs in the Whitecap Knoll flora (Table 2).

CF. ROSACEAE JUSSIEU, 1789  
MORPHOTYPE TRL 12

FIG. 6A, B

**Referred specimen**—UF 256-21552.

**Description**—Lamina elliptic, symmetrical, unlobed, small, length 32 mm, width 27 mm, l/w ratio 1.1, leaf area estimate 575 mm<sup>2</sup>, petiole missing; lamina apex round; base round; margin serrate, teeth compound, with two orders of teeth, 1–2 on proximal side and one on distal side of major teeth, close, regularly spaced, apices acute and sometimes glandular; sinuses angular; venation pinnate; midvein moderately thick, straight; secondary venation semicraspedodromous, spacing regular, excurrent attachment, angle of divergence 56–67°, course slightly curved towards apex; secondaries with exmedial branching of tertiary veins that enter major teeth; usually one intersecondary per intercostal extending <½ to margin before merging with tertiary vein; tertiary venation mixed percurrent; higher order venation reticulate.

**Discussion**—The presence of small, closely spaced teeth, tooth apices rounded and glandular (Fig. 6A), and semicraspedodromous secondaries (Fig. 6B) suggest Rosaceae (Meyer and Manchester 1997). This leaf differs from *Amelanchier* by its relatively straight secondary course, and purely reticulate tertiary veins.

SAPINDALES JUSSIEU EX BERCHTOLD & J. PRESL, 1820  
CF. MELIACEAE JUSSIEU, 1789  
MORPHOTYPE TRR 05

FIG. 7K

**Referred specimen**—UF 256-20809.

**Description**—Winged seed with elongate lateral wing in plane of symmetry adjoining an elliptical seed body; length 4.4 mm, width 2.4 mm; apex obtuse; base acute; proximal convex, distal irregular; wing base extends to near seed body base on distal side; wing veinless, surface possibly punctate; nutlet length 2 mm, width 1.3 mm, markedly oblique (41°) to wing mid-line, apex obtuse.

**Discussion**—This specimen (Fig. 7K) is similar to extant *Chukrasia* A. Jussieu (1830) (Meliaceae), in shape, margin, seed body angle and surface texture but it is about half as big, the apex is acute and proximal margin of the wing is not as thickened as in *Chukrasia*. This specimen is similar to fossil *Cedrela merrillii* but it lacks the marginal vein. It is distinct from the unidentified winged seeds in the Whitecap Knoll flora (figs. 8 P, Q in [Manchester 2000](#)). The meliaceous genus *Cedrela* is found in the Sumner Spring flora (Table 2, [Smith et al. 1998](#)).

RUTACEAE/SIMAROUBACEAE  
*CHANEYA* WANG & MANCHESTER, 2000

*CHANEYA TENUIS* (LESQUEREUX) WANG & MANCHESTER,  
2000

FIG. 5Q

*Chaneya tenuis* (Lesquereux) [Wang and Manchester, 2000](#), *Int. J. Plant Sci.* 161, pgs. 169–173, figs. 2, 3.

**Basionym**—*Porana tenuis* [Lesquereux, 1883](#), *Rep. U.S. Geol. Surv. Terr.*, p. 173.

**Referred specimens**—UF 256-20825–20837, 20839, 20840, 34081, 34082, 34084.

**Description**—Fruits with accrescent five-lobed, hypogynous calyx; diameter 1.4–2.5 cm ( $x=2$ ,  $N=15$ ); sepals entire-margined, elliptical to obovate, apex rounded, with glands or resin bodies; sinus between sepals acute, incised to near central disk; sepals with primary radiating venation, each with three primary veins, midvein stronger than successively weaker outer pairs; primary veins diverging from central disk and extend in a straight course, sometimes dichotomizing near upper margin, forming loops with adjacent primary veins; primary veins joined by secondary arched cross veins; occasional sepals with two extra primary veins extend  $>1/2$  length of sepal; central thickened disk with globose fruit body.

**Discussion**—A formal description of these fruits as *Chaneya tenuis* was presented by [Wang and Manchester \(2000\)](#), with half the number of Eocene North American specimens in that article being from Teater Road. These fruits (Fig. 5Q) have likely affinities with Simaroubaceae ([Wang and Manchester 2000](#)) or the closely related family Rutaceae ([Teodoridis and Kvaček 2005](#)). *Chaneya* can

also be found in Ruby Basin, Beaverhead Basins, and Florissant flora (Table 2) as well as Eocene and Miocene sites in China ([Wang and Manchester 2000](#)) and Miocene of Europe ([Manchester and Zastawniak 2007](#), [Teodoridis and Kvaček 2005](#)).

UNKNOWN DICOTYLEDONEAE [RAY, 1686–1704](#)

INDET. ORDER

MORPHOTYPE TRR 06

FIG. 7I

**Referred specimens**—UF 256-20925, 20926, 20928–20934, 20936–20942, 20944, 20945, 20947–20949, 21407b, 21568a, 21570, 21571, 34087, 34093, 34110.

**Description**—Thin textured bracts or bracteoles, ovate, elliptic, circular or obovate, asymmetrical or symmetrical, length 5–10 mm ( $x=8$ ,  $N=26$ ), width 3–7 mm ( $x=5$ ,  $N=27$ ), l/w ratio 1–2.5, lamina area estimate 11–43 mm<sup>2</sup> ( $x=27$ ,  $N=25$ ); apex acute or obtuse; base obtuse, cuneate, or truncate, symmetrical or asymmetrical, sometimes with slightly overlapping margins; margin entire; primary veins campylodromous, 9–11, sometimes branching; interconnecting veins are acute angled and join adjacent primary vein; surface sometimes with circular structures.

**Discussion**—These little laminae appear to be bracts or bud scales, sometimes with an overlapping margin (Fig. 7I), but we have been unable to determine their affinity. There is a superficial resemblance to the bladder-like fruit of *Humulus* L. (1753), but these are flat, rather than tubular structures ([Tembrock et al. 2016](#)). *Ostrya virginiana* (Mill.) K. Koch (1873) also has similar size fruit involucre with campylodromous primary veins but the interconnecting veins are usually at right angles to primary veins and there is no evidence for a nutlet in our fossils.

INDET. FAMILY

*ANTHOLITHES* SCHLOTHEIM EX [BRONGNIART, 1822](#)

*ANTHOLITHES* SP.

FIG. 7A

**Referred specimens**—UF 256-20738, 21579b.

**Description**—Flower pedicellate, length 7–8 mm, width 2.8–4 mm; hypanthium subtending five sepaloid structures; sepaloid structures punctate, length ~2.1–2.4 mm; pedicel 4.1–4.7 mm long.

**Discussion**—The presence of a five-parted pedicellate flower with a hypanthium (Fig. 7A) suggests Rosaceae and Rhamnaceae ([Judd et al. 1999](#)). These characters, along with glandular sepals (punctuate in the fossil specimen) suggest Rosaceae ([Rydberg 1921](#)), while in

Rhamnaceae, the sepals lack glands, but the flowers do have a nectariferous disk (Brizicky 1964) not observed in our specimens. Until a thorough investigation is performed that might allow better resolution of the affinities of these specimens, we prefer to assign them in the form genus *Antholithes* (Becker 1961).

*BECKEROSPERMA* MEYER & MANCHESTER, 1997

*BECKERSOPERMA OVALICARPA* (BECKER) MEYER & MANCHESTER, 1997

FIG. 7L

**Referred specimens**—UF 256-21030–21033, 21035.

**Description**—Winged seed; elliptic; length 7–11 mm ( $x=8$ ,  $N=5$ ), width 1.3–6 mm ( $x=5$ ,  $N=5$ ); apex rounded or truncate; base rounded; margin entire; central body pyriform or oval, length 2.7–4.5 mm ( $x=3.8$ ,  $N=3$ ), width 2.4–3.1 mm ( $x=2.8$ ,  $N=3$ ); apex acute; base rounded, oblique ( $25^\circ$ ) to wing midline; wing veinless.

**Discussion**—This winged seed type (Fig. 7L), of unknown familial affinity, is particularly common in the Bridge Creek flora (Meyer and Manchester 1997), and is found in the Sumner Spring, Whitecap Knoll, and Mormon Creek floras (Table 2, Becker 1960).

INDET. GEN ET SP.

MORPHOTYPE TRR 07

FIG. 7D, 7E

**Referred specimens**—UF 256-20737a.

**Description**—Branched system with two sessile infructescences; infructescence length 6–7 mm ( $x=6.5$ ,  $N=2$ ), width 5–5.5 mm ( $x=5.2$ ,  $N=2$ ); fruits elliptic, length 3.7–5.5 mm ( $x=4.7$ ,  $N=3$ ), width 2.2–4.4 mm ( $x=3.2$ ,  $N=3$ ); apex sharply acute; base rounded.

**Discussion**—This structure (Fig. 7D) is superficially similar to *Ostrya virginiana*, but infructescences of *O. virginiana* are pedunculate, and each fruit has longitudinal veins converging to a sharply acute apex. Each infructescence in our specimen consists of a solid structure subtending disaggregating bract-like structures or seeds.

MORPHOTYPE TRR 08

FIG. 7N

**Referred specimen**—UF 256-21010.

**Description**—Pedicellate drupe; fruit body wide-elliptical, with a hard elliptical endocarp, surrounded by flattened remains of a fleshy mesocarp/exocarp; length 4 mm, width 3.6 mm; apex retuse; base cuneate; pedicle length 1.4 mm; endocarp with at least two, single seeded locules.

**Discussion**—A fruit of similar size, shape, and two

locules was attributed to *Amelanchier grayi* Chaney (1927) (Chaney 1927, pl. 14 fig. 5), without a description, and is considered as indeterminate (Meyer and Manchester 1997). The drupes of *Amelanchier* are usually similar in size and shape (Fig. 7N), and hold 4–10, single seeded locules, as exemplified by *A. laevis* Weigand (1912) (Jones 1946).

MORPHOTYPE TRR 09

FIG. 5M

**Referred specimens**—UF 256-21011, 21012.

**Description**—Samara; asymmetrical, with a single lateral wing, length 10–13 mm ( $x=12$ ,  $N=2$ ), width 5.1–6 mm ( $x=5.8$ ,  $N=2$ ); distal margin of wing with two rounded lobes separated by a broad v-shaped notch, base acute and cuneate; lateral margins of wing concave on pedicel side, convex on stelar side. Wing margins thickened with a fimbrial vein; wing with subparallel sinuous longitudinal vein; wing length 9 mm ( $N=2$ ), width 6 mm ( $N=2$ ). Seed body obpyriform, length 4.3–6.4 mm ( $x=5.4$ ,  $N=2$ ), width 3.2–4.2 mm ( $x=3.7$ ,  $N=2$ ); apex rounded; proximal margin nearly straight, with persistent style about 0.5 mm long; seed body axis forming  $15^\circ$  angle to the long axis of the wing; pedicel or stipe length  $\sim 3.5$  mm.

**Discussion**—The distinctive features of this samara include the straight proximal margin, prominent distal margin, and small persistent style (Fig. 5M). The nearly straight proximal margin suggests that this is a mericarp of a schizocarpic fruit, as occurs in many Sapindaceae. The narrow basal extension resembles a pedicel, but there is no indication of perianth scar at base of the nutlet, so it may instead represent a stipe. Mirle and Burnham (1999) surveyed asymmetrical samaras of extant angiosperms with particular attention to the New World, but this fossil does not conform to any of the genera they treated.

MORPHOTYPE TRL 13

FIG. 6N, 6O

**Referred specimen**—UF 256-21545.

**Description**—Lamina lanceolate, symmetrical, unlobed, small, length 72 mm, width 19 mm, l/w ratio 3.7, leaf area estimate 905 mm<sup>2</sup>, petiole missing; lamina apex attenuate; base acute; margin serrate; teeth simple, irregularly spaced, distant, apices acute, distal flank concave, proximal flank straight or convex; sinuses rounded; venation pinnate, midvein weak, straight; secondary venation semicraspedodromous, ca. ten pairs, spacing irregular, with excurrent attachment, angle of divergence  $32\text{--}72^\circ$ , course broadly looping; tertiary venation

alternate percurrent; epimedial tertiaries obtuse on one side of midvein, acute on other side of midvein, distal course basiflexed; quaternary veins reticulate.

**Discussion**—The presence of semicraspedodromous venation, percurrent tertiaries, and size of the teeth (Fig. 60) suggest Juglandaceae, but weak preservation of this specimen does not allow for confident assignment.

MORPHOTYPE TRR 10

FIG. 7R

**Referred specimens**—UF 256-21026–21029, 20748b, 21576.

**Description**—Fruit widely elliptic; length 11–20 mm ( $x=14$ ,  $N=6$ ), width 8–15 mm ( $x=11$ ,  $N=6$ ); apex rounded with small protuberance; base rounded; surface reticulate, with transverse to oblique partitions; pedicel length 4.5 mm, width 4.3 mm, striated.

**Discussion**—These fruits appear to have a longitudinal furrow on one surface (Fig. 7R). Specimen UF 256-21576 shows striations near the apex that lead to a small protuberance.

MORPHOTYPE TRR 11

FIG. 7C

**Referred specimens**—UF 256-20921, 20922.

**Description**—Fruit samaroid; elliptic, straight, length at least 17 mm, width 4.2–5.5 mm ( $x=4.9$ ,  $N=2$ ); apex and base acute; margins shallow convex, one of the lateral margins thickened. Wing with faint transverse veins. Seed body fusiform with longitudinal grooves, with its long axis forming an obtuse angle with the long axis of the wing.

**Discussion**—This specimen (Fig. 7C) may be a one-seeded fabaceous fruit with the greater portion forming a wing for wind dispersal, somewhat similar to extant *Mora* Bentham (1839) (Gunn 1991).

MORPHOTYPE TRR 12

FIG. 7F, G

**Referred specimen**—UF 256-20735.

**Description**—Infructescence paniculate; 13 mm long, 10 mm wide, bearing fusiform fruits, 2.1 mm long, 1.0 mm wide; infructescence stems with alternate, reduced leaves.

**Discussion**—Preliminary discussions suggest that this specimen (Fig. 7F) might represent Podostemaceae (W. Judd, personal communication, 2024).

MORPHOTYPE TRR 13

FIG. 7H

**Referred specimen**—UF 256-20814.

**Description**—Fruit; elliptic, length 6 mm, width 2.5 mm; rounded at one end, pointed at the other; a broad conical “cap” with a different texture from the rest of the fruit culminates in the pointed end; longitudinal furrow along one margin.

**Discussion**—This fruit (Fig. 7H) impression bears a strong resemblance to extant *Mastixia* (Cornales). Comparable fruits of extant *Mastixia* are illustrated by Manchester and Collinson (2019, Pl. 1, figs. 1, 6).

MORPHOTYPE TRR 14

FIG. 7J

**Referred specimen**—UF 256-20751.

**Description**—Infructescence; elliptic, length 9 mm, width 5.2 mm, composed of overlapping bracts; bracts triangular, apex acute, one bract length 2.4 mm, width 1.2 mm; pedicel overlapping infructescence, length 8 mm, width 1.5 mm.

**Discussion**—An infructescence with overlapping triangular bracts, attached to a pedicel (Fig. 7J), is similar to the fossil *Joffrea* Crane and Stockey (1985), although the size of UF 256-20751 is half that of *Joffrea* (Crane and Stockey 1985). Presently, there are no cercidiphyllaceous types of leaves in the Teater Road locality. There is some similarity with extant *Ostrya virginiana* but the infructescence size of *O. virginiana* is 3x of UF 256-20751, bract size is 5–8x of 20751, and the bracts are apiculate in *O. virginiana*. Specimen UF 256-21039 is of a similar size and shape and may contain overlapping bracts as in 20751.

MORPHOTYPE TRR 15

FIG. 7M

**Referred specimen**—UF 256-21574.

**Description**—Scale; oblong, length 6.2 mm, width 4.3 mm; apex truncate, with thickened margin of possible ventral protuberance; base truncate; margins straight; scale with medial line, possibly degraded showing longitudinal striations.

**Discussion**—This may be the impression of the dorsal side of a coniferous scale (Fig. 7M).

MORPHOTYPE TRR 16

FIG. 7O

**Referred specimen**—UF 256-21009.

**Description**—Pedicellate fruit; fruit body elliptic, length 5 mm, width 3 mm; stigma persistent; surface tuberculate; pedicel striate, length 11 mm, width 1 mm, with slightly enlarged node.

## MORPHOTYPE TRR 17

FIG. 7P

**Referred specimen**—UF 256-21016.**Description**—Pyriform structure, length 23 mm, width 12 mm, l/w ratio 1.9; apex acute, base truncate.**Discussion**—This specimen has depth and transverse fractures suggesting a woody nut-like structure (Fig. 7P).

## MORPHOTYPE TRR 18

FIG. 7S

**Referred specimen**—UF256-21052.**Description**—Ellipsoidal seed/fruit, length 2.6 mm, width 4.2 mm; apex round, base asymmetrically cordate; structure with three concentric arcs, with radiating striations extending from base to first arch.

## MORPHOTYPE TRR 19

FIG. 6R

**Referred specimen**—UF256-21049.**Description**—Winged seed, elliptic, length 15 mm, width 4 mm, wing extending laterally from seed body; apex obtuse; base acute; proximal and distal straight; wing base extends to  $\frac{1}{3}$  of seed body on distal side; wing with striations extending upward along proximal margin from seed body apex; seed body oval, length 6 mm, width 3 mm; striations evident near seed body apex, base arched.

## MORPHOTYPE TRR 20

FIG. 7B

**Referred specimen**—UF 256-21008.**Description**—Flower pedicellate, diameter 4.0 mm, height 3.0 mm, with two 2-merous, hypogynous perianth whorls; calyx two, persistent, boat shaped, length 1.8 mm, borne on receptacle, height 0.7 mm; petals two, oblong, length 2.3 mm, width 0.6 mm; ovary ovate, length 2.2 mm, width 1.0 mm, with thick style and capitate stigma; 12 stamens, filament length 7.8 mm, anther ellipsoid, length 0.5 mm, width 0.3 mm, dorsifixed; pedicel length 2.7 mm.

## FAUNA

## CYCLOID FISH SCALE

**Referred specimens**—UF 256-20706b, 20812, 20815, 20819b, 20951d, 21119b, 21403b, 34119b, 59621b, c, 79031b, 78153b, Fish Scale 1–3, 5.**Description**—Scale; elliptic to oval, length 3–7 mm, width 2.5–3.2 mm; scale with tightly packed ridges in a circular pattern.**Discussion**—Disarticulated cycloid-like fish scales are

found at Beaverhead Basins (Becker 1969), and various fish scales are known from Whitecap Knoll, Ruby Basin and York Ranch (Becker 1961, 1973, Manchester 2000, Retallack et al. 2000).

## CTENOID FISH SCALE

**Referred specimen**—Fish Scale 4.**Description**—Scale; elliptic, length >6.0 mm, width 6.0 mm; scale with relatively wide, semi-circular ridges interspersed among numerous, thinner, tightly packed semicircular ridges.

## TRICHOPTERA KIRBY, 1813

## TERRINDUSIA SP.

**Referred specimen**—UF 256-20749.**Description**—Elongate larval case; length 14.0 mm, width 6.0 mm; case composed of large stones basal to smaller stones apically, and organic material.**Discussion**—The use of sand grains and organic material (Fig. 6S) is similar to *Terrindusia* Vialov (1973) in Dilcher and Lott (2005). To date, this is the only Trichoptera Kirby sample discovered at Teater Road, or any other Late Eocene site of Central Oregon (Retallack et al. 2000). Trichoptera have also been found at Ruby Basin and Beaverhead Basins (Becker 1969). Other insect parts found at Teater Road include wings, an abdomen, and a beetle elytra.

## DISCUSSION

The Teater Road plant assemblage represents a pond deposit including the floating aquatic plants *Salvinia*, and *Ceratophyllum*, and marginal wetland plants such as *Typhoides* and *Decodon*, but the assemblage is dominated by non-aquatic trees and shrubs. Conifers include Pinaceae and possibly Cupressaceae. Deciduous trees and shrubs include members of Platanaceae, Rosaceae, Ulmaceae, Betulaceae, Fagaceae, Juglandaceae, Fabaceae, and Sapindaceae. Lianas are represented by the leaves of *Smilax* and *Toxicodendron*. Only a few broad-leaved evergreen plants, such as *Mahonia* and possibly Lauraceae were identified. Monocots include possible Poaceae, *Typhoides* (cf. *Typha* or *Sparganium*) and *Smilax*. Only a single moss specimen was observed (*Archaeomnium*). The flora is dominated by temperate taxa that conform to the category of mixed Mesophytic Forest (Wang 1961, Wolfe 1979), such as *Acer*, *Alnus*, *Cercis*, *Craigia*, *Dipteronia*, *Fraxinus*, *Hydrangea*, *Koelreuteria*, and *Ulmus*. Extant genera in the Teater Road flora that are no longer native in North America today include *Ailanthus*, *Craigia*, *Dipteronia*, *Koelreuteria*, and *Paliurus*. Other items found

in the Teater Road shales include occasional remains of fish, insects, and bird feathers.

Similar warm temperate or subtropical vegetation is suggested by taxonomic composition of nearby Late Eocene petrified woods, which include *Platanus*, *Quercus* and *Ulmus* (Wheeler et al. 2006, 2023; Wheeler and Manchester 2007, 2021).

### Comparison with other western North American Eocene to Oligocene floras

For a comparison of the Teater Road floristic composition, the following western North American floras were selected: Middle Eocene: Clarno Nut Beds, Oregon (Manchester 1981, 1994), Green River Formation (Parachute Creek Member, as known from sites in Colorado and Utah, Brown 1934, MacGinitie 1969); Late Eocene: Gray Butte, Oregon (Ashwill 1983, McFadden 1986, Smith et al. 1998), Whitecap Knoll, Oregon (Manchester 2000), Mormon Creek, Montana (Becker 1960), Metzel Ranch, Montana (Becker 1972), Ruby, Montana (Becker 1961), Florissant, Colorado (Britton and Hollick 1907, MacGinitie 1953, Manchester and Crane 1983, 1987, Manchester 2001, Meyer 2003); Early Oligocene: York Ranch, Montana: Becker (1973), Beaverhead Basins, Montana (Becker 1969), and Bridge Creek, Oregon (Chaney 1927, Meyer and Manchester 1997) (Table 2).

Of particular interest are the assemblages of regional proximity to Teater Road, i.e., the Gray Butte (Sumner Spring), Whitecap Knoll and Bridge Creek floras. Among these, the number of shared species or morphotypes ranges from 16 to 19 in the Late Eocene floras (Gray Butte and Whitecap Knoll, respectively), with examples including *Dipteronia brownii* and *Florissantia ashwillii*. A greater number (32) are shared with the more diverse Early Oligocene Bridge Creek flora. Twelve taxa are shared among the Teater Road, Whitecap Knoll and Bridge Creek floras, i.e., *Daphnogene*, *Mahonia*, *Platanus*, *Alnus*, *Quercus*, *Paleocarya*, *Decodon*, *Acer*, *Dipteronia*, *Florissantia*, *Ulmus*, and *Beckerosperma*. The Middle Eocene Nut Beds flora also includes some genera in common with the Teater Road flora, including *Pinus*, *Daphnogene*, *Platanus*, *Quercus*, *Palaeocarya*, *Rhus*, *Hydrangea*, *Deviacer* and *Cedrelospermum*. Expanding out to all our selected western North American sites, we find *Typha*-like leaves are shared widely across Teater Road, Sumner Spring, Metzel Ranch, Ruby Basin, York Ranch, Beaverhead Basins, Bridge Creek, and Florissant. *Mahonia* is shared across all the sites except for York Ranch. Angiosperms unique to Teater Road and the Late Eocene of western United States are cf. *Acrocarpus*, cf. *Crataegus*,

*Rutaspermum*, and *Davidia* (Table 2). These observations may provide a record of floral transition in midlatitude western North America during the Late Eocene time, from subtropical to predominantly temperate character.

### Comparison with other floras near Post, Oregon

Other fossil floras near Teater Road include the Oligocene Crooked River assemblage (Chaney 1927) about 4 km to the southwest, which is considered part of the broader Bridge Creek flora (Meyer and Manchester 1997) and the Late Eocene silicified fruit, seed and wood assemblages about 13–15 km to the west, near the town of Post. Although the Teater Road flora is limited to impression fossils in shale, the Post Hammer (UF loc. 279) and Dietz Hill (UF loc. 278) sites include 3-dimensionally preserved silicified fruits and seeds, many of which have been identified to the generic level (Manchester and McIntosh 2007), and anatomically preserved silicified woods, many of which also have been described taxonomically (Wheeler and Manchester 2007, 2021; Wheeler et al. 2023). The fossil wood assemblages from these two sites are consistent with warm temperate to possibly subtropical vegetation (Wheeler and Manchester 2021; Wheeler et al. 2023). Table 3 lists the silicified fruits and woods identified from localities 278 and 279 for comparison with the Teater Road impression fossils. These floras are likely to be similar in age but they reflect different taphonomic biases.

### Extinct vs extant taxa

The Teater Road flora includes many genera that are still extant today, namely *Salvinia*, *Pinus*, *Picea*, *Smilax*, *Mahonia*, *Platanus*, *Parrotia*, *Ribes*, *Cercis*, *Gymnocladus*, *Acrocarpus*, *Paliurus*, *Amelanchier*, *Crataegus*, *Ulmus*, *Alnus*, *Carpinus*, *Quercus*, *Decodon*, *Rhus*, *Toxicodendron*, *Cedrela*, *Acer*, *Dipteronia*, *Koelreuteria*, *Ailanthus*, *Craigia*, *Hydrangea*, *Davidia*, *Eucommia* and *Fraxinus*. However, at this time in the Late Eocene there were also many genera that are now extinct. Examples include *Cedrelospermum*, *Paleocarya*, *Rutaspermum*, *Deviacer*, *Plafkeria*, *Florissantia*, *Flectorivus*, *Chaneya* and *Beckerospermum*. There are still other taxa that could not be confidently identified relative to extant genera, due to convergence in leaf form across unrelated taxa today. Examples include *Laurophyllum*, *Daphnogene* and *Typhoides*.

### Biogeographic considerations: exotic vs endemic taxa

Several of the Teater Road genera are east Asian in their distribution today: *Dipteronia*, *Ailanthus*, *Koelreuteria*,

*Eucommia* and *Craigia*. *Trochodendron*, known locally from silicified wood (Wheeler and Manchester 2021), also fits this pattern (Wheeler and Manchester 2021). *Decodon* is endemic to eastern North America today, while *Mahonia* and *Hydrangea* are found today both in eastern Asia and North America. *Paliurus* is no longer present in North America, but is shared today between Europe and Asia. These fit the pattern of many taxa that were formerly widespread in the northern hemisphere whose geographic ranges have been reduced to refugial areas in response to late Cenozoic climate change (Manchester 1999, Manchester et al. 2009, Donoghue and Smith 2004).

### Climatic interpretations

We base our inferences about the climate of Teater Road on comparisons with extant angiosperm relatives and on leaf physiognomy. The Nearest Living Relative approach infers paleoclimate based on the modern-day climates where related taxa live today (e.g., Peppe et al. 2011). The Teater Road assemblage has 26 taxa that can tolerate a temperate climate, four that are tropical, two that are mediterranean, and one that is cosmopolitan (Table 1).

For estimates of Mean Annual Temperature (MAT) based on foliar physiognomy, we tabulated proportions of entire-margined leaves among the 40 species/morphotypes of dicotyledonous foliage from Teater Road (Appendix 2). Of these, 14, or 35%, are entire-margined whereas the others are serrate-margined. Using the regressions for mean annual temperature (MAT) provided by Wolfe (1979) and Wing and Greenwood (1993) i.e.,  $MAT=0.306(35)+1.14$ , Wilf (1997) i.e.,  $MAT=0.286(35)+2.24$ , Miller et al. (2006) i.e.,  $MAT=0.2899(35)+1.32$ , and Peppe et al. (2011) i.e.,  $MAT=0.204(35)+4.6$  we obtained estimates of 11.9, 12.3, 11.5 and 11.7°C respectively; the average of these estimates is 11.9 °C (53.4 °F). Using the CLAMP methodology (Wolfe 1971, Spicer 2011–2024) we obtained a cooler MAT estimate of 10.4 °C (50.7 °F). By contrast, the modern-day mean annual temperature for Bend, Oregon (~87 km from Teater Road) for the period of 1990–2016 is 8.3 °C (47.0 °F), with extreme maximum temperature reaching 38.3 °C (101.0 °F) and extreme minimum temperature reaching -27.8 °C (-18.0 °F) (NOAA, 2021).

Surprisingly, the more inland floras of Ruby, and Metzel Ranch, Montana, which were presumably at higher elevation, were calculated by CLAMP methodology to have warmer MAT of 12.2 and 13.1 °C, respectively (Lielke et al. 2012). Out of curiosity, we recomputed MAT for Ruby,

using the proportions of entire vs serrate dicotyledonous morphotypes indicated in Table 1 of Lielke et al. (2012). Based on our calculation of (7/49=12 % entire-margined, and using the same regressions applied for the Teater Road analysis presented above, we obtained significantly cooler values of 4.8, 5.7, 4.8, and 7.0°C. For Metzel Ranch, applying the same methodology with reference to Table 1 of Lielke et al. (2012) and the source monograph of Becker (1972), lead us to MAT estimates of 8.6, 9.4, 8.6, and 9.7°C. These results suggest that the analyses of Lielke et al. (2012) need to be repeated with more care in examining the original material and using the improved CLAMP modern comparative dataset now available (Spicer 2011–2024).

To infer Mean Annual Precipitation (MAP) for the Teater Road flora, we calculated the average leaf blade area (mm<sup>2</sup>, length x width x 2/3) and mean of the natural logarithms (MlnA) for the 39 dicotyledonous leaf species that were sufficiently complete for estimating lamina area (one species was excluded due to having only the lower portion of the lamina) (Supplemental Table 2). Following the direct measure equation of Wilf et al. (1998),  $\ln(MAP)=0.548 \cdot MlnA + 0.768$ , we obtained an MAP estimate of 71 cm per year (+30/-20 cm). The recent mean annual average precipitation for Bend, Oregon, from 1990–2018 is 26.9 cm (NOAA 2021). The relatively low mean leaf area for Teater Road may indicate adaptation for a dry climate, as earlier suggested in reference to the study of *Cercis* leaves and fruits by Jia and Manchester (2014).

During the transition from Middle to Late Eocene floras in Oregon, the taxonomic composition in this region shifted from subtropical (Clarno Nut Beds) to warm/cool temperate taxa including dry-adapted components at we see in the Teater Road flora, consistent with prior observations on other Paleogene western North American floras (Chaney 1948, Wolfe 1979, Manchester 1994, DeVore and Pigg 2010, Wheeler et al. 2023). This shift agrees with the inferred MAT of Teater Road (11.9°C) as temperate, while Sumner Springs (7.6°C) and Whitecap Knoll (9.0°C) would be considered paratemperate as defined by Wolfe (1979).

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### LITERATURE CITED

- Adroit, B., X. Zhuang, T. Wappler, J.-F. Terral and B. Wang. 2020. A case of long-term herbivory specialized feeding trace on *Parrotia* (Hamamelidaceae) plant species. *Royal Society Open Science* 7:201449. [<http://dx.doi.org/10.1098/rsos.201449>].
- Andrews, H.N., C.A. Arnold, E. Boureau, J. Doubringer and S. Leclercq. 1970. *Traité de Paléobotanique*, Volume IV, Fascicule I, Filicophyta. Masson et Cie, Paris. 519 pp.
- Arnold, C.A. 1936a. Some fossil species of *Mahonia* from the Tertiary of eastern and southeastern Oregon. *Contributions from the Museum of Paleontology* 5(4):57–66.
- Arnold, C.A. 1936b. The occurrence of *Cedrela* in the Miocene of Western America. *The American Midland Naturalist* 17(6): 1018–1021.
- Arnold, C.A. 1952. Tertiary plants from North America II. Fossil capsule valves of Koelreuteria from the John Day Series of Oregon. *Palaeobotanist* 1: 74–78.
- Arnott, G.A.W. 1838. Observations of some new or obscure species of plants. *Magazine of Zoology and Botany* 2:543–552.
- Ashwill, M. 1983. Seven fossil floras in the rain shadow of the Cascade Mountains, Oregon. *Oregon Geology* 45(10):107–111.
- Axelrod, D.I. 1940. The Pliocene Esmeralda flora of west-central Nevada. *Journal of the Washington Academy of Sciences* 30: 163–172.
- Axelrod, D.I. 1944. The Alvord Creek flora. Pp. 225–262 in R.W. Chaney, C. Condit and D.I. Axelrod. (eds.). *Pliocene floras of California and Oregon*. *Carnegie Institute of Washington Publications*, 553, Washington, D.C.
- Axelrod, D.I. 1966. The Eocene Copper Basin flora of northeastern Nevada. *University of California Publications, Geological Sciences* 59:1–125.
- Axelrod, D.I. 1986. Cenozoic history of some western American pines. *Annals of the Missouri Botanical Garden* 73(3):565–641.
- Axelrod, D.I. 1995. The Miocene Purple Mountain flora of western Nevada. *University of California Publications, Geological Sciences* 139:1–62.
- Axelrod, D.I. 1998. The Oligocene Haynes Creek flora of eastern Idaho. *University of California Publications, Geological Sciences* 143:1–99.
- Baillon, H.E. 1871. Sur deux nouveaux genres Apetales. *Adansonia* 10:110–119.
- Becker, H.F. 1960. The Tertiary Mormon Creek flora from the Upper Ruby River Basin in southwestern Montana. *Palaeontographica, Abt. B* 107(4–6):83–126.
- Becker, H.F. 1961. Oligocene plants from the Upper Ruby River Basin, south-western Montana. *Geological Society of America Memoir* 82:1–127.
- Becker, H.F. 1966. Additions to and revision of the Oligocene Ruby Paper Shale flora of southwestern Montana. *Contributions from the Museum of Paleontology* 20(5):89–119.
- Becker, H.F. 1969. Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. *Palaeontographica, Abt. B* 127:1–142.
- Becker, H.F. 1972. The Metzel Ranch flora of the Upper Ruby River Basin, southwestern Montana. *Palaeontographica, Abt. B* 141:1–61.
- Becker, H.F. 1973. The York Ranch flora of the Upper Ruby River Basin, southwestern Montana. *Palaeontographica, Abt. B* 143:1–93.
- Berchtold, F.G. von, J.S. Presl. 1820. O Prirozenosti Rostlin. Prazei.
- Berry, E.W. 1925. A new *Salvinia* from the Eocene. *Torreya* 25(6):116–118.
- Berry, E.W. 1926. Tertiary floras from British Columbia, Canada. *Canada Department of Mines Bulletin* 42: 91–116, 153–171.
- Berry, E.W. 1929. A revision of the flora of the Latah Formation. *United States Geological Survey Professional Paper* 154-H:225–264.
- Bierhorst, D.W. 1971. *Morphology of Vascular Plants*. The Macmillan Company, New York. 560 pp.
- Blanchard, J., H. Wang and D.L. Dilcher. 2016. Fruits, seeds and flowers from the Bovay ad Bolden clay pits (early Eocene Tallahatta Formation, Claiborne Group), northern Mississippi, USA. *Palaeontologia Electronica* 19.3.51A. [<https://doi.org/10.26879/579>].
- Boulter, M.C. and Z. Kvacek. 1989. The Palaeocene flora of the Isle of Mull. *Palaeontological Association Special Papers Palaeontology* 42:1–149.
- Britton, E.G. and A. Hollick. 1907. American fossil mosses, with description of a new species from Florissant, Colorado. *Bulletin of the Torrey Botanical Club* 34(3):139–142.
- Brizicky, G.K. 1964. The genera of Rhamnaceae in the Southeastern United States. *Journal of the Arnold Arboretum* 45(4):439–463.
- Bromhead, E.F. 1838. An attempt to ascertain characters of the botanical alliances. *Edinburgh New Philosophical Journal* 25:123–133.
- Brongniart, A. 1822. Sur la classification et la distribution des végétaux fossils en général, et sur ceux des terrains de sédiment supérieur en particulier. *Mémoires du Muséum d'Histoire Naturelle* 8:203–240.
- Brown, R. 1818a. Narrative of a journey in the interior of China. Appendix. Longman, Hurst, Rees, Orme, Brown, London.
- Brown, R. 1818b. Narrative of an Expedition to Explore the River Zaire. Appendix. John Murray, London.
- Brown, R.W. 1934. The recognizable species of the Green River flora. *United States Geological Survey Professional Paper* 185-C:45–68.
- Brown, R.W. 1935. Miocene leaves, fruits, and seeds from Idaho, Oregon, and Washington. *Journal of Paleontology* 9(7):572–587.
- Brown, R.W. 1937. Further additions to some fossil floras of the western United States. *Washington Academy of Sciences Journal* 27:506–577.
- Brown, R.W. 1940. New species and changes of name in some American fossil floras. *Journal of Washington Academy of Sciences* 30(8):344–356.
- Browne, P. 1756. *The Civil and Natural History of Jamaica*. T. Osborne and J. Shipton, London.
- Buechler, W.K. 2014. Variability of venation patterns in extant genus *Salix*: Implications for fossil taxonomy. *PaleoBios*

- 30(3):89–104.
- Burge, D.O. and S.R. Manchester. 2008. Fruit morphology, fossil history, and biogeography of *Paliurus* (Rhamnaceae). *International Journal of Plant Sciences* 169:1066–1085.
- Burnham, R.J. 1986. Foliar morphological analysis of the Ulmoideae (Ulmaceae) from the Early Tertiary of Western North America. *Palaeontographica, Abt. B* 201:135–167.
- Cain, S.A. and G.M.O. Castro. 1959. Manual of vegetation analysis. Harper and Brothers, New York. 329 pp.
- Call, V.B. and D.L. Dilcher. 1992. Investigations of angiosperms from the Eocene of southeastern North America: samaras of *Fraxinus wilcoxiana* Berry. *Review of Palaeobotany and Palynology* 74:249–266.
- Call, V.B. and D.L. Dilcher. 1994. *Parvileguminophyllum coloradensis*, a new combination for *Mimosites coloradensis* Knowlton, Green River Formation of Utah and Colorado. *Review of Palaeobotany and Palynology* 80(3–4):305–310.
- Call, V.B. and D.L. Dilcher. 1997. The fossil record of *Eucommia* (Eucommiaceae) in North America. *American Journal of Botany* 84(6):798–814.
- Candolle, A.P. de. 1805. Flore Francaise. Troisieme Edition 4(2). Du Fouds de H. Agasse, Paris.
- Candolle, A.P. de. 1811. Monographie des Ochnacées et des Simaroubées. Nouveau Bulletin des Sciences, Societe Philomatique de Paris, series 2:206–209.
- Candolle, A.P. de and C.P.J. Sprengel. 1821. Elements of the philosophy of plants. W. Blackwood, Edinburgh.
- Cardoso, D.B.O.S., L.P. De Queiroz and H.C. Lima. 2014. A taxonomic revision of the South American papilionoid genus *Luetzelburgia* (Fabaceae). *Botanical Journal of the Linnean Society* 175:328–375.
- Carpenter, R.J., G.J. Jordan and R.S. Hill. 2007. A toothed Lauraceae leaf from the early Eocene of Tasmania, Australia. *International Journal of Plant Sciences* 168:1191–1198.
- Chaney, R.W. 1927. Geology and Paleontology of the Crooked River Basin, with special reference to the Bridge Creek. *Carnegie Institute of Washington Publications* 346:45–138.
- Chaney, R.W. 1948. The Ancient Forests of Oregon. Condon Lectures. Oregon State System of Higher Education, Eugene. 56 pp.
- Chaney, R.W. and D.I. Axelrod. 1959. Miocene floras of the Columbia Plateau. *Carnegie Institution of Washington Publications* 617:1–237.
- Chen, X.H., K.L. Xiang, L. Lian, H.W. Peng, A.S. Erst, X.G. Xiang, Z.D. Chen and W. Wang. 2020. Biogeographic diversification of *Mahonia* (Berberidaceae): Implications for the origin and evolution of East Asian subtropical evergreen broadleaved forests. *Molecular Phylogenetics and Evolution* 151: <https://doi.org/10.1016/j.ympev.2020.106910>.
- Collinson, M.E. 2001. Cainozoic ferns and their distribution. *Brittonia* 53:173–235.
- Collinson, M.E. and H.J. Gregor. 1988. Rutaceae from the Eocene of Messel, West Germany. *Tertiary Research* 9(1–4):67–80.
- Collinson, M.E., S.R. Manchester and V. Wilde. 2012. Fossil fruit-sand seeds of the Middle Eocene Messel biota, Germany. *Abhandlungen der Senckenberg Gesellschaft für Naturforschung* 570: 1–251, 76 pl.
- Conran, J.G., R.J. Carpenter and G.J. Jordan. 2009. Early Eocene *Ripogonum* (Liliales: Ripogonaceae) leaf macrofossils from southern Australia. *Australian Systematic Botany* 22:219–228.
- Conwentz, H. 1886. Die Flora des Bernsteins II. Die Angiospermen des Bernsteins. Danzig. 140 pp.
- Corbett, S.L. and S.R. Manchester. 2004. Phytogeography and fossil history of *Ailanthus* (Simaroubaceae). *International Journal of Plants Sciences* 165:671–690.
- Crane, P.R. and R.A. Stockey. 1985. Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the Late Paleocene of Alberta, Canada. *Canadian Journal of Botany* 63:340–364.
- Cronquist, A., A. Takhtajan, and A. Zimmermann. 1966. On the higher taxa of Embryobionta. *Taxon* 15(4): 129–134.
- Delaude, C. 1993. Les Sapindaceae et leurs saponines. *Bulletin de la Société Royale des Sciences de Liège* 62:93–120.
- De Lima, H.C. 1980. Revisão taxonômica do Gênero *Vataireopsis* Ducke (Leg. Fab.). *Rodriguésia* 32(54):21–40.
- Denk, T. and R.M. Dilhoff. 2005. *Ulmus* leaves and fruits from the Early-Middle Eocene of northwestern North America: systematics and implications for character evolution within Ulmaceae. *Canadian Journal of Botany* 83:1663–1681.
- Desfontaines, R.L. 1788. Memoire sur un nouveau genre d'arbre. *Ailanthus glandulose*, *l'Ailanthus glanduleux*. *Histoire de l'académie royale des sciences; avec les mémoires de mathématique & de physique*. 265–270.
- DeVore, M.L. and K. B. Pigg. 2010. Floristic composition and comparison of middle Eocene to late Eocene and Oligocene floras in North America. *Bulletin of Geosciences, Czech Geological Survey* 85(1): 111–134.
- Dietrich, A.G. 1824. Flora der Gegend um Berlin 1(2). G.C. Nauck, Berlin.
- Dilcher, D.L. and T.A. Lott. 2005. A middle Eocene fossil plant assemblage (Powers Clay Pit) from western Tennessee. *Bulletin of the Florida Museum of Natural History* 45(1):1–43.
- Ding, H.B., B. Yang, S.S. Zhou, M.B. Maw, K.W. Maung and Y.H. Tan. 2019. New contributions to the flora of Myanmar. *Plant Diversity* 41(3):135–152.
- Ding, S.-T., B.-N. Sun, J.-Y. Wu and X.-C. Li. 2011. Miocene *Smilax* leaves and associated epiphyllous fungi from Zhejiang, East China and their paleoecological implications. *Review of Palaeobotany and Palynology* 165:209–223.
- Ding, W.N., J. Huang, T. Su, Y.W. Xing and Z.K. Zhou. 2018. An early Oligocene occurrence of the palaeoendemic genus *Dipteronia* (Sapindaceae) from Southwest China. *Review of Palaeobotany and Palynology* 249:16–23.
- Donoghue, M.J. and S.A. Smith. 2004. Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359(1450):1633–1644.
- Dumortier, B.C.J. 1829. Analyse des Familles des Plantes. De J. Casterman, Tournay.
- Edwards, W.N. 1927. The occurrence of *Koelreuteria* (Sapindaceae) in Tertiary rocks. *Journal of Natural History* 20:109–112.
- Ellis, B., D.C. Daily, L.J. Hickey, K.R. Johnson, J.D. Mitchell, P. Wilf and S.L. Wing. 2009. Manual of leaf architecture. Cornell University Press, Ithaca. 190 pp.
- Engler, H.G.A. 1892. Syllabus der Vorlesungen über Specielle und Medicinisch-Pharmaceutische Botanik. Gebrüder Borntraeger, Berlin.
- Engler, H.G.A. 1907. Syllabus der Pflanzenfamilien, 5<sup>th</sup> ed. Gebrüder Borntraeger, Berlin.
- Ettingshausen, C. 1853. Die Tertiäre flora Häring in Tirol. Aus der K.K. Hof- Und Staatsdruckerel, Wien.

- Fields, P.F. 2021. Resurrection of the Miocene Flannelbush as *Fremontodendron lobatum* (Malvaceae). *Phytoneuron* 28:1–6.
- Fritsch, P.W., C.F. Nowell, S.T. Leatherman, W. Gong, B. Cruz, D.O. Burge and A. Delgado-Salinas. 2018. Leaf adaptations and species boundaries in North American *Cercis*; implications and species boundaries in North America. *American Journal of Botany* 105:1577–1594.
- Global Biodiversity Information Facility (GBIF). 2021. [<https://www.gbif.org> accessed November 2021].
- Gmelin, J.F. 1791. *Systema naturae per regna tria naturae*. Volume 1, Part 2. Georg. Emanuel, Leipzig.
- Gorozhankin, I.N. 1904. Lektsii po morfologii i sistematike archegonialnykh rastenij. II. Pteridophyta, I-Archisporae. Mamontov, Moscow.
- Gray, S.F. 1822. *A Natural Arrangement of British Plants*. Vol. 2. Baldwin, Cradock and Joy, London.
- Gregor, H.-J. 1975. Die Rutaceen aus dem Mittel-Miozän der Oberpfälzer Braunkohle. *Courier Forschungs Institut Senckenberg* 54:1–118.
- Gregory-Wodzicki, K.M. 2000. Relationships between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras. *Paleobiology* 26:668–688.
- Güner, T.H. and T. Denk T. 2012. The genus *Mahonia* in the Miocene of Turkey: Taxonomy and biogeographic implications. *Review of Palaeobotany and Palynology* 175:32–46.
- Gunn, C.R. 1991. Fruits and seeds of genera in the subfamily Caesalpinioideae (Fabaceae). *United States Department of Agriculture, Technical Bulletin* 1755:1–408.
- Herendeen, P.S. 1992. The fossil history of the Leguminosae from the Eocene of Southeastern North America: Pp. 85–160 in P.S. Herendeen and D.L. Dilcher (eds.). *Advances in Legume Systematics: Part 4. The Fossil Record*. The Royal Botanic Gardens, Kew.
- Herendeen, P.S., D.H. Les and D.L. Dilcher. 1990. Fossil *Ceratophyllum* (Ceratophyllaceae) from the Tertiary of North America. *American Journal of Botany* 77(1):7–16.
- Hergert, H.L. 1961. Plant fossils in the Clarno Formation, Oregon. *Ore Bin* 2:55–62.
- Hermesen, E.J. 2005. The Fossil Record of Iteaceae and Grossulariaceae in the Cretaceous and Tertiary of the United States. PhD dissertation, Cornell University, Ithaca, New York.
- Herrera, F., M.R. Carvalho, S.L. Wing, C. Jaramillo and P.S. Herendeen. 2019. Middle to Late Paleocene Leguminosae fruits and leaves from Colombia. *Australian Systematic Botany* 32:385–408.
- Hickey, L.J. 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60:17–33.
- Hickey, L.J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of Western North Dakota. *The Geological Society of America Memoir* 150:1–181.
- Hickey, L.J. and R.K. Peterson. 1978. *Zingiberopsis*, a fossil genus of the ginger family from Late Cretaceous to early Eocene sediments of Western Interior North America. *Canadian Journal of Botany* 56(9):1136–1152.
- Hill, R.S. 1986. Lauraceous leaves from the Eocene of Nerriga, New South Wales. *Alcheringa* 10: 327–351.
- Hoffmannsegg, J.C. von and J.H.F. Link. 1809. *Flore portugaise ou description de toutes*. Vol. 1. Charles Frédéric Amelang, Berlin.
- Hollick, A. 1894. Fossil *Salvinias* including description of a new species. *Bulletin of the Torrey Botanical Club* 21:253–257.
- Hou, D. 1994. Studies in Malesian Caesalpinioideae (Leguminosae). I. The genera of *Acrocarpus*, *Afzelia*, *Copaifera*, and *Intsia*. *Blumea* 38:313–330.
- Hu, Q., J. Huang, Y.-F. Chen and S.R. Manchester. 2017. *Mahonia* fossils from the Oligocene of South China: Taxonomic and biogeographic implications. *Palaeoworld* 26:691–698.
- Huang, J., T. Su, J. Lebeeton-Anberree, S.-T. Zhang and Z.-K. Zhou. 2016. The oldest *Mahonia* (Berberidaceae) fossil from East Asia and its biogeographic implications. *Journal of Plant Research* 129:209–223.
- Jia, H. and S.R. Manchester. 2014. Fossil leaves and fruits of *Cercis* L. (Leguminosae) from the Eocene of western North America. *International Journal of Plant Sciences* 175(5):601–612.
- Jia, L.B., T. Su, Y.J. Huang, F.X. Wu, T. Deng and Z.K. Zhou. 2019. First fossil record of *Cedrelospermum* (Ulmaceae) from the Qinghai-Tibetan Plateau: Implications for morphological evolution and biogeography. *Journal of Systematics and Evolution* 57(2):94–104.
- Jijina, A.P., E.D. Currano and K. Constenius. 2019. The paleobotany and paleoecology of the Eocene Herren Beds of north-central Oregon, USA. *Palaios* 34(9):424–436.
- Jones, G.N. 1946. *American species of Amelanchier*. The University of Illinois Press, Urbana. 126 pp.
- Judd, W.S., C.S. Campbell, E.A. Kellogg and P.F. Stevens. 1999. *Plant Systematics, A Phylogenetic Approach*. Sinauer Associates, Inc., Sunderland. 464 pp.
- Jussieu, A.L. de. 1789. *Genera Plantarum*. Apud Viduam Herissant, Parisiis.
- Kirby, W. 1813. *Strepsiptera*, a new order of insects proposed; and the characters of the order, with those genera, laid down. *Transactions of the Linnean Society* 2:86–122.
- Kirchner, W.C.G. 1898. Contributions to the fossil flora of Florissant, Colorado. *Transactions of the Academy of Sciences St. Louis* 8:161–188.
- Kirkbride, J.H., Jr., C.R. Gunn and A.L. Weitzman. 2003. Fruits and seeds of genera in the subfamily Faboideae (Fabaceae). *United States Department of Agriculture, Technical Bulletin* 1890:1–635.
- Klucking, E.P. 1959. The fossil Betulaceae of western North America. Master's Thesis, University of California, Berkeley.
- Knowlton, F.H. 1898. The fossil plants of the Payette Formation. *United States Geological Survey, 18th Annual Report Pt. 3*:721–744.
- Knowlton, F.H. 1900. Fossil plants of the Esmeralda Formation. *United States Geological Survey Annual Report* 21.
- Knowlton, F.H. 1902. Fossil flora of the John Day Basin Oregon. *United States Geological Survey Bulletin* 204:1–153.
- Kral, R. 1993. *Pinus*. Pp. 373–398 in *Flora of North America* Editorial Committee (ed.). *Flora of North America Vol. 2*. Oxford University Press, New York.
- Kvaček, Z. 1971. Fossil Lauraceae in the stratigraphy of the North-Bohemian Tertiary. *Sborník Geologických Ved Paleontologie* 13:47–86.
- Kvaček, Z., C. Bůžek and S.R. Manchester. 1991. Fossil fruits of Pteleaceae Weyland-Tiliaceae, not Sapindaceae. *Botanical Gazette* 152(4):522–523.
- Kvaček, Z., S.R. Manchester and M.A. Akhmetiev. 2005. Review of the fossil history of *Craigia* (Malvaceae s.l.) in the Northern Hemisphere based on fruits. Pp. 114–140 in M.A. Akhmetiev and A.B. Herman (eds.). *Modern Problems of Paleofloristics*,

- Palaeophytogeography and Phytostatigraphy. GEOS, Moscow.
- Lamarck, J.B.A.P.M. de. 1785. Encyclopédie méthodique: botanique. Volume 1, issue 2. Paris.
- LaMotte, R.S. 1952. Catalogue of the Cenozoic plants of North America through 1950. *The Geological Society of America Memoir* 51:1–381.
- Laxmann, E.G. 1772. Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae 16.
- Lepage, B.A. 2001. New species of *Picea* A. Dietrich (Pinaceae) from the middle Eocene of Axel Heiberg Island, Arctic Canada. *Botanical Journal of the Linnean Society* 135:137–167.
- Lesquereux, L. 1878. Contributions to the fossil flora of the Western Territories, part II. The Tertiary Flora. *United States Geological Survey of the Territories* 7:1–366.
- Lesquereux, L. 1883. Contributions to the fossil flora of the western Territories, Part III, The Cretaceous and Tertiary floras. Report of the United States Geological Survey of the Territories 8: 1–283.
- Lesquereux, L. 1888. Specimens of fossil plants collected at Golden, Colorado, 1883, for the Museum of Comparative Zoology at Cambridge, Mass. *Bulletin of the Museum of Comparative Zoology at Harvard College* 16:43–60.
- Les, D.H. 1988. The Evolution of achene morphology in *Ceratophyllum* (Ceratophyllaceae), II. Fruit variation and systematics of the "spiny-margined" group. *Systematic Botany* 13 (1): 73–86.
- Lestiboudois, T.G. 1826. Botanique Élémentaire ou Principes de Botanique D'Anatomie et de Physiologie Végétale. Roret, Paris.
- Lielke, K., S.R. Manchester and H. Meyer. 2012. Reconstructing the environment of the northern Rocky Mountains during the Eocene/Oligocene transition: constraints from the palaeobotany and geology of south-western Montana, USA. *Acta Palaeobotanica* 52(2):317–358.
- Lindley, J. 1830. An Introduction to the Natural System of Botany. Longman, Rees, Orme, Brown and Green, London.
- Lindley, J. 1836. A Natural System of Botany. 2 ed. Longman, Rees, Orme, Brown, Green and Longman, London.
- Lindley, J. 1846. The Vegetable Kingdom. Bradbury and Evans, London.
- Link, J.H.F. 1829. Handbuch zur Erkennung der nutbarsten und am häufigsten vorkommenden Gewächse 2. Berlin.
- Link, J.H.F. 1833. Hortus Regius Botanicus Berolinensis. Apud G. Reimer. Berloini.
- Linnaeus, C. 1753. Species Plantarum. Holmiae, Laurentii Salvii.
- Litke, R. 1968. Über den Nachweis tertiärer Gramineen. *Sonderdruck aus Monatsberichte der Deutschen Akademie der Wissenschaften zu Berlin* 10(6):462–471.
- Little, E.L., Jr. and W.B. Critchfield. 1969. Subdivisions of the genus *Pinus* (pines). *United States Division of Agriculture Forest Service Miscellaneous Publication* 1144:1–51.
- Liu, X., S.R. Manchester and J. Jin. 2014. *Alnus* subgenus *Alnus* in the Eocene of Western North America based on leaves, associated catkins, pollen, and fruits. *American Journal of Botany* 101(11):1925–1943.
- Luo, Y. and Z-K. Zhou. 2002. Leaf architecture in *Quercus* subgenus *Cyclobalanopsis* (Fagaceae) from China. *Botanical Journal of the Linnean Society* 140:283–295.
- Mabberley, D.J. 1993. The Plant-Book, A portable dictionary of the higher plants. Cambridge University Press, Cambridge. 707 pp.
- Macginitie, H.D. 1937. The flora of the Weaverville beds of Trinity County, California; with descriptions of the plant-bearing beds. *Carnegie Institution of Washington Publication* 465:83–151.
- Macginitie, H.D. 1953. Fossil plants of the Florissant beds of Colorado. *Contributions to Paleontology, Carnegie Institution of Washington Publication* 599:1–198.
- Macginitie, H.D. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Sciences* 83:1–140.
- Macoboy, S. 1991. What tree is that? Crescent Books, New York. 367 pp.
- Manchester, S.R. 1981. Fossil plants of the Eocene Clarno Nut Beds. *Oregon Geology* 43:75–81.
- Manchester, S.R. 1986. Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America. *International Journal of Plant Sciences* 147(2):200–226.
- Manchester, S.R. 1987a. Extinct ulmaceous fruits from the Tertiary of Europe and western North America. *Review of Palaeobotany and Palynology* 52:119–129.
- Manchester, S.R. 1987b. The fossil history of the Juglandaceae. *Monographs in Systematic Botany, Missouri Botanical Gardens* 21:1–137.
- Manchester, S.R. 1989a. Systematics and fossil history of the Ulmaceae: Pp. 221–251 in P.R. Crane and S. Blackmore (eds.). Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 2: 'Higher' Hamamelidae. Clarendon Press, Oxford.
- Manchester, S.R. 1989b. Attached reproductive and vegetative remains of the extinct American-European genus *Cedrelospermum* (Ulmaceae) from the Early Tertiary of Utah and Colorado. *American Journal of Botany* 76:256–276.
- Manchester, S.R. 1992. Flowers, fruits, and pollen of *Florissantia*, an extinct malvacean genus from the Eocene and Oligocene of Western North America. *American Journal of Botany* 79:996–1008.
- Manchester, S.R. 1994. Fruits and seeds of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon. *Palaeontographica Americana* 58:1–205.
- Manchester, S.R. 1999. Biogeographical relationships of North America Tertiary flora. *Annals of the Missouri Botanical Gardens* 86:472–522.
- Manchester, S.R. 2000. Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. *Oregon Geology* 62:51–63.
- Manchester, S.R. 2001. Update on the megafossil flora of Florissant, Colorado. *Denver Museum of Nature & Science Series* 4:137–161.
- Manchester, S.R. and M.E. Collinson. 2019. Fruit morphology, anatomy and relationships of the type species of *Mastixicarpum* and *Eomastixia* (Cornales) from the late Eocene of Hordle, southern England. *Acta Palaeobotanica* 59:51–67.
- Manchester, S.R. and P.R. Crane. 1983. Attached leaves, inflorescences, and fruits of *Fagopsis*, an extinct genus of fagaceous affinity from the Oligocene Florissant flora of Colorado, USA. *American Journal of Botany* 70:1147–1164.
- Manchester, S.R. and P.R. Crane. 1987. A new genus of Betulaceae from the Oligocene of Western North America. *Botanical Gazette* 148(2):263–273.
- Manchester, S.R. and W.S. Judd, 2022. *Loxopteroides weeksae* gen. et sp. nov. (Anacardiaceae) samaras and associated foliage from the Eocene of western North America. *Acta Palaeobotanica* 62:1–10.
- Manchester, S.R. and W.C. McIntosh. 2007. Late Eocene silicified

- fruits and seeds from the John Day Formation near Post, Oregon. *PaleoBios* 27:7–17.
- Manchester, S.R. and E. Zastawniak. 2007. Fruit with perianth remains of *Chaneya* Wang & Manchester (Extinct Rutaceae) in the Upper Miocene of Sos'nica, Poland. *Acta Palaeobotanica* 47:253–259.
- Manchester, S.R., Z.-D. Chen, A.-M. Lu and K. Uemura K. 2009. Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. *Journal of Systematics and Evolution* 47(1):1–42. DOI: 10.1111/j.1759-6831.2009.00001.x
- Manchester, S.R., F. Grimsson and R. Zetter. 2015. Assessing the fossil record of Asterids in the context of our current phylogenetic framework. *Annals of the Missouri Botanical Garden* 100:329–363. DOI: 10.3417/2014033
- Martinov, I.I. 1820. Tekhno-Botanicheskii Slovar: na latinskom i rossiiskom iazykakh. St. Petersburg.
- Mathewes, R, S.B. Archibald and A. Lundgren. 2021. Tips and identification of early Eocene *Fraxinus* L. samaras from the Quilchena locality, Okanagan Highlands, British Columbia, Canada. *Review of Palaeobotany and Palynology* 293:104480.
- McClain, A.M. and S.R. Manchester. 2001. *Dipteronia* (Sapindaceae) from the Tertiary of North America and implications for the phytogeographic history of the Aceroideae. *American Journal of Botany* 88(7):1316–1325.
- Mcfadden, J.J. 1986. Fossil flora near Gray Butte, Jefferson County, Oregon. *Oregon Geology* 48:51–55, 58.
- Medikus, F.K. 1789. Philosophische Botanik: mit kritischen Bemerkungen. Von den mannigfaltigen Umhüllungen der Saamen. Erstes Stück. Vol. 1. Neue Hof- und Akademische Buchhandlung.
- Meyer, C.A. von. 1831. Verzeichniss der pflanzen, welche während der, auf Allerhochsten Befehl, in den Jahren 1829 und 1830 unternommenen Reise im Caucasus und in den Provinzen am westlichen Ufer des Caspischen Meeres. Gedruckt in der Buchdruckerei der Kaiserl Akademie der Wissenschaften, St. Petersburg.
- Meyer, H.W. 2003. The Fossils of Florissant. Smithsonian Institution, Washington, D.C. 258 pp.
- Meyer, H.W. and S.R. Manchester. 1997. The Oligocene Bridge Creek Flora of the John Day Formation, Oregon. *University of California Publications, Geological Sciences* 141:1–195.
- Miller, I.M., M.T. Brandon and L.J. Hickey. 2006. Using leaf margin analysis to estimate Mid-Cretaceous (Albian) paleolatitude of the Baja BC Block. *Earth Planetary Science Letters* 245:95–114.
- Miller, N.G. 1980. Fossil Mosses of North America and their significance. Pp. 9–39 in R.J. Taylor and A.E. Leviton, A.E. (eds.). *The Mosses of North America*. Pacific Division, American Association for the Advancement of Science, San Francisco.
- Miller, P. 1754. *The Gardeners Dictionary*. Abridged. 4<sup>th</sup> ed., vol. 3. P. Miller, London.
- Miquel, F.A.W. 1855. *Flora van Nederlandsch Indie* 1(1). Tribus Millettieae. C.G. van der Post, Amsterdam.
- Mirbel, C.F.B. de. 1815. *Elemens de Physiologie Vegetale et de Botanique*. Chez Magimel, Paris.
- Mirle, C. and R.J. Burnham. 1999. Identification of asymmetrically winged samaras from the Western Hemisphere. *Brittonia* 51:1–14.
- Monroe, S. 1981. Late Oligocene-Early Miocene facies and lacustrine sedimentation, Upper Ruby River Basin, southwestern Montana. *Journal of Sedimentary Petrology* 51:939–951.
- Mu, X.-Y., J.-X. Li, X.-F. Xia and L.-C. Zhao. 2015. Cupules and fruits of *Lithocarpus* (Fagaceae) from the Miocene of Yunnan, southwestern China. *Taxon* 64:795–808.
- Mustoe, G.E. 2002. *Hydrangea* fossils from the Early Tertiary Chuckanut Formation. *Washington Geology* 30(3):17–20.
- Myers, J.A. 2006. The latest Eocene Badger's Nose flora of the Warner Mountains, northeast California: the "in between" flora. *PaleoBios* 26(1):11–29.
- Myers, J.A. and D.M. Erwin. 2015. *Deviacer pidemarmanii* sp. nov. (Polygalaceae) from the Late Eocene-Early Oligocene Badger's nose Paleoflora, Modoc County, California. *International Journal of Plant Sciences* 176(3):259–268.
- National Oceanic and Atmospheric Administration (NOAA). 2021. National Environment Satellite, Data, and Information Service. [<https://www.nesdis.noaa.gov/>. accessed 19 January 2021].
- Nauman, C.E. 1993. Salviaceae. Pp. 336–337 in *Flora of North America* Editorial Committee (eds.). *Flora of North America North of Mexico*, Volume 2. Oxford University Press, New York.
- Newberry, J.S. 1898. The later extinct flora of North America. *United States Geological Survey Monograph* 35:1–295.
- Nuttall, T. 1818. *The Genera of North American Plants* 1. D. Heartt, Philadelphia.
- Oliver, D. 1890. *Hooker's Icones Plantarum*. Williams and Norgate, Edinburgh.
- Peppe, D.J., A. Baumgartner, A. Flynn and B. Blonder. 2018. Reconstructing paleoclimate and paleoecology using fossil leaves. Pp. 289–317 in D. Croft, D. Su and S. Simpson (eds), *Methods in paleoecology*. Springer, Cham.
- Peppe, D.J., D.L. Royer, B. Cariglina, S.Y. Oliver, S. Newman, E. Leight, G. Enikolopov, M. Fernandez-Burgos, F. Herrera, J.M. Adams, E. Correa, E.D. Currano, J.M. Erickson, L.F. Hinojosa, J.W. Hoganson, A. Iglesias, C.A. Jaramillo, K.R. Johnson, G.J. Jordan, N.J.B. Kraft, E.C. Lovelock, C.H. Lusk, Ü Niinemets, J. Penuelas, G. Rapson, S.L. Wing and I.J. Wright. 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimate applications. *New Phytologist* 190:724–739.
- Perleb, K.J. 1818. Versuch über die Arzneikräfte der Pflanze. Heinrich Remigius Sauerländer.
- Pérez-Consuegra, N., A. Cuervo-Gomez, C. Martinez, C. Montes, F. Herrera, S. Madrinan and C. Jaramillo. 2017. Paleogene *Salvinia* (Salviaceae) from Colombia and their paleobiogeographic implications. *Review of Palaeobotany and Palynology* 246:85–108.
- Perleb, K.J. 1826. *Lehrbuch der Naturgeschichte des Pflanzenreichs*. Druck und Verlag von Friedrich Wagner.
- Pigg, K.B., S.R. Manchester and W.C. Wehr. 2003. *Corylus*, *Carpinus*, and *Palaeocarpinus* (Betulaceae) from the Middle Eocene Klondike Mountain and Allenby Formations of Northwestern North America. *International Journal of Plant Sciences* 164:807–822.
- Potbury, S.S. 1935. The La Porte flora of Plumas County, California. *Carnegie Institution of Washington Publication* 465:30–81.
- PoWO (2023–2024). "Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; [<http://www.plantsoftheworldonline.org> retrieved February 2023 and April 2024].
- Radford, A.E., W.C. Dickison, J.R. Massey and C.R. Bell. 1974. *Vascular Plant Systematics*. Harper and Row, New York. 891 pp.
- Radlkofer, L.A.T. 1879. *Ueber die Sapindaceen* Hollandisch-Indiens. Reprinted from *Actes Congres International de Botanists*. Amsterdam 1877: 70–133.
- Ramirez, J.L. and R.S. Cevallos-Ferriz. 2000. Leaves of Berberidaceae

- (*Berberis* and *Mahonia*) from the Oligocene sediments, near Tepexi de Rodríguez, Puebla. *Review of Palaeobotany and Palynology* 110:247–257.
- Raunkiaer, C. 1934. The use of leaf size in biological plant geography. Pp. 368–378 in C. Raunkiaer (ed.). *The Life Forms of Plants and Statistical Geography*. Clarendon Press, Oxford.
- Ray, J. 1686–1704. *Historia plantarum: species hactenus editas aliasque insuper multas noviter inventas & descriptas complectens*. Mariae Clark, London.
- Read, R.W. and L.J. Hickey. 1972. A revised classification of fossil palms and palm-like leaves. *Taxon* 21:129–137.
- Reichenbach, H.G.L. 1832. *Flora Germanica Ecursoria* 2(2). Lipsiae, Carolum Cnobloch.
- Retallack, G.J., E.A. Bestland and T.J. Fremd. 2000. Eocene and Oligocene paleosols of Central Oregon. *The Geological Society of America Special Paper* 344:1–192.
- Robertson, K.R., J.B. Phipps and J.R. Rohrer. 1992. Summary of leaves in the genera of Maloideae (Rosaceae). *Annals of the Missouri Botanical Garden* 79:81–94.
- Rudolphi, F.C.L. and F.K.L. Rudolphi. 1830. *Systema orbis vegetabilium: quod gratiosi medicorum ordinis consensu et auctoritate*. Kunike.
- Rydberg, A. 1921. Notes on Rosaceae-XIII. *Bulletin of the Torrey Botanical Club* 48(6):159–172.
- Saint-Hilarie, J.H.J. 1805. *Exposition des Familles Naturelles et de la Germination des Plantes*. Vol. 2. Treuttel et Würtz.
- Samuels, J.X. and J. Cavin. 2013. The earliest known fisher (Mustelidae), a new species from the Rattlesnake Formation of Oregon. *Journal of Vertebrate Paleontology* 33(2):448–454.
- Saporta, G. 1865. Études sur la végétation du sud-est de la France à L'époque tertiaire. *Annals des Sciences Naturelles*, 5e Series 4(1):5–64.
- Saporta, G. 1873. Études sur la Végétation de sud-est de la France à L'époque Tertiaire Su:lement I; Révision de Flora des Gypes d'Aix. *Annales des Sciences Naturelles* 5e serie 18:23–146.
- Saporta, G. 1888. Dernieres Adjonctions a la Flora Fossile D'Aix-En-Provence. *Annals des Sciences Naturelles*, 7e Series 7(1):5–104.
- Sargent, C.S. 1933. *Manual of the trees of North America*. The Riverside Press, Cambridge. 910 pp.
- Schimper, W.P. 1879. *Handbuch der Palaeontologie, Abtheilung Paleophytologie* 1. R. Oldenbourg, München.
- Schorn, H.E. 1966. Revision of the fossil species of *Mahonia* from North America. Master's Thesis, University of California, Berkeley.
- Schultze-Motel, J. 2003. *Fossilium Catalogus II: Plantae pars 106*. Index of generic names of fossil plants, 1979–2000. Backhuys Publishers, Leiden. 218 pp.
- Scopoli, J.A. 1760. *Flora Carniolica*. 414. J.Th. Trattner, Viennae.
- Séguier, J.F. 1754. *Plantae Veronenses seu Stirpium quae in Agro Veronensi Reperiuntur Methodica Synopsis*. 3. Verona.
- Shahbaz, S.E. and N.M. Shareef. 2018. Use of morphological and anatomical characters to delimit varieties of *Paliurus spinachristi* Mill. (Rhamnaceae). *Innovaciencia* 6(2):1–14.
- Small, J.K. 1903. *Flora of the Southeastern United States*. J.K. Small, New York.
- Smiley, C.J. and L.M. Huggins. 1981. *Pseudofagus idahoensis* n. gen. et sp. (Fagaceae) from the Miocene Clarkia Flora. *American Journal of Botany* 68:741–761.
- Smith, G.A., S.R. Manchester, M. Ashwill, W.C. Mcintosh and R.M. Conrey. 1998. Late Eocene-early Oligocene tectonism, volcanism, and floristic change near Gray Butte, central Oregon. *Geological Society of America Bulletin* 100:759–778.
- Smith, W.W. and W.E. Evans. 1921. *Craigia*, a new genus of Sterculiaceae. *Transactions and Proceedings of the Botanical Society of Edinburgh* 28:69–71.
- Soltis, D., P. Soltis, P. Endress, M. Chase, S.R. Manchester, W. Judd, L. Majure and E. Mavrodiev. 2018. *Phylogeny and Evolution of the Angiosperms*. The University of Chicago Press, Chicago, 580 pp.
- Spicer, R.A. 2011–2024. CLAMP on-line: [http://clamp.ibcas.ac.cn/CLAMP\\_Home.html](http://clamp.ibcas.ac.cn/CLAMP_Home.html). Accessed April 2024.
- Spicer, R. A., P.J. Valdes, T.E.V. Spicer, H.J. Craggs, G. Srivastava, R.C. Mehrotra and J. Yang. 2009. New developments in CLAMP: calibration using global gridded meteorological data. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 283(1-2):91–98
- Steere, W.C. 1946. Cenozoic and Mesozoic bryophytes of North America. *American Midland Naturalist* 36:298–324.
- Sun, X.-Q., J.-Y. Xue, Z. Lei, M.-M. Li, Y.-M. Zhang, G.-C. Zhou and Y.-Y. Huang. 2018. Taxonomic and phylogenetic significance of leaf venation characteristics in *Dioscorea* plants. *Archives of Biological Science* 70(2):397–407.
- Tanai, T. 1961. Neogene floral change in Japan. *Journal of the Faculty of Science Hokkaido University, Series IV. Geology and Mineralogy* 11:119–398.
- Tanai, T. and J.A. Wolf. 1977. Revisions of *Ulmus* and *Zelkova* in the middle and late Tertiary of western North America. *Geological Survey Professional Paper* 1026:1–14.
- Taylor, R.J. 1993. *Picea*. Pp. 369–373 in *Flora of North America* Editorial Committee (eds.). *Flora of North America*, Vol. 2. Oxford University Press. New York.
- Tembrock, L.R., J.M. Mcaleer and T.M. Gilligan. 2016. A revision of native North American *Humulus* (Cannabaceae). *Journal of the Botanical Research Institute of Texas* 10(1):11–30.
- Teodoridis, V. and Z. Kvaček. 2005. The extinct genus *Chaneya* Wang & Manchester in the Tertiary of Europe - a revision of *Porana*-like fruit remains from Ohningen and Bohemia. *Review of Palaeobotany and Palynology* 134:85–103.
- Tiffney, B.H. 1980. Fruits and seeds of the Brandon Lignite, V. Rutaceae. *Journal of the Arnold Arboretum* 61:1–36.
- Trelease, W. 1918. *The Ancient Oaks of America*. Brooklyn Botanic Garden Memoirs 1.
- Tropicos.Org. Missouri Botanical Garden. [<http://www.tropicos.org> accessed 29 Mar 2021].
- Unger, F. 1845. *Studii si Cercetari, Stiintele Naturii*, Nr. 2:43–51.
- Unger, F. 1847. *Chloris Protogaea*. *Beitrag zur flora der vorwelt*. W. Engelmann, Leipzig.
- Unger, F. 1850. *Die fossile Flora von Sotzka*. *Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe* 2:3–67.
- van Der Burgh, J. 2005. *Fossilium Catalogus II: Plantae pars 107*. Index of Angiosperm leaf species names. A–B, 1823–2000. Backhuys Publishers, Leiden. 143 pp.
- van Der Burgh, J. 2006. *Fossilium Catalogus II: Plantae pars 108*. Index of Angiosperm leaf species names. C, 1823–2005. Backhuys Publishers, Leiden. 162 pp.
- van Der Burgh, J. 2008. *Fossilium Catalogus II: Plantae pars 109*. Index of Angiosperm leaf species names. D–G, 1823–2006. Backhuys Publishers, Leiden. 153 pp.
- van Der Burgh, J. 2010. *Fossilium Catalogus II: Plantae pars 110*. Index of Angiosperm leaf species names. H–L, 1823–2008. Backhuys Publishers, Leiden. 126 pp.

- van Der Burgh, J. 2011. Fossilium Catalogus II: Plantae pars 111. Index of Angiosperm leaf species names. M–O, 1823–2008. Backhuys Publishers, Kerkwerve. 116 pp.
- van Der Burgh, J. 2013. Fossilium Catalogus II: Plantae pars 112. Index of Angiosperm leaf species names. P, 1823–2011. Backhuys Publishers, Leiden. 159 pp.
- van Der Burgh, J. 2016. Fossilium Catalogus II: Plantae pars 113. Index of Angiosperm leaf species names. S–Z, 1823–2014. Backhuys Publishers, Leiden. 184 pp.
- van Roosmalen, M.G.M. 1985. Fruits of the Guianan Flora. Institute of Systematic Botany, Utrecht University, Netherlands.
- Ventenat, E.P. 1799. Tableau du Regne Vegetal, selon de Methode de Jussieu. Vol. 2. J. Drissonnier, Paris.
- von Humboldt, F.W.H.A., A.J.A. Bonpland, and K.S. Kunth. 1822. Nova genera et species plantarum 2. Lutetiae Parisiorum.
- Wang, Chi-Wu. 1961. The forests of China with a survey of grassland and desert vegetation. Maria Moors Cabot Foundation publication no. 5, Cambridge. 313 pp.
- Wang, L., Q.-Q. Xu and J.-H. Jin. 2014. A reconstruction of the fossil *Salvinia* from the Eocene of Hainan Island, South China. *Review of Palaeobotany and Palynology* 203:12–21.
- Wang, Q., S.R. Manchester, H.-J. Gregor, S. Shen and Z.-Y. Li. 2013. Fruits of *Koelreuteria* (Sapindaceae) from the Cenozoic throughout the Northern Hemisphere: Their ecological, evolutionary, and biogeographic implications. *American Journal of Botany* 100:422–449.
- Wang, Y. and S.R. Manchester. 2000. *Chaneya*, a new genus of winged fruit from the Tertiary of North America and Eastern Asia. *International Journal of Plant Sciences* 161:167–178.
- Webb, L.J. 1959. A physiognomic classification of Australian rain forests. *Journal of Ecology* 47:551–570.
- Wheeler, E.A. and S.R. Manchester. 2002. Woods of the Eocene Nut Beds flora, Clarno Formation, Oregon, USA. *International Association of Wood Anatomists Journal, Supplement* 3. 188 pp.
- Wheeler, E.A. and S.R. Manchester. 2007. Review of the wood anatomy of extant Ulmaceae as context for new reports of late Eocene *Ulmus* woods. *Bulletin of Geosciences* 82(4):329–342. DOI: 10.3140/bull.geosci.2007.04.329.
- Wheeler, E.A. and S.R. Manchester. 2021. A diverse assemblage of late Eocene woods from Oregon, western USA. *Fossil Imprint* 77(2):299–329.
- Wheeler, E.A., S.R. Manchester and P. Baas. 2023. A late Eocene wood assemblage from the Crooked River Basin, Oregon, USA. *PaleoBios* 40(14):1–55.
- Wheeler, E.A., S.R. Manchester and M. Wiemann. 2006. Eocene woods of central Oregon. *PaleoBios* 26(3):1–6.
- Wilde, V. and Manchester, S.R., 2003. *Cedrelospermum* fruits (Ulmaceae) and related leaves from the Middle Eocene of Messel (Hesse, Germany). *Courier-Forschungsinstitut Senckenberg* 241: 147–154.
- Wilf, P. 1997. When are leaves good thermometers? A new case for leaf margin analysis. *Paleobiology* 23:373–390.
- Wilf, P., K.C. Beard, K.S. Davies-Vollum and J.W. Norejko. 1998. Portrait of a Late Paleocene (Early Clarkforkian) Terrestrial Ecosystem: Big Multi Quarry and Associated Strata, Washakie Basin, Southwestern Wyoming. *Palaios* 13(6):514–532.
- Wing, S.L. and D.R. Greenwood. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. *Philosophical Transactions of the Royal Society of London B* 341:243–252.
- Wolfe, J.A. 1964. Miocene floras from Fingerrock Wash Southwestern Nevada. *Geological Survey Professional Paper* 454-N:1–36.
- Wolfe, J. A. 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 9(1):27–57
- Wolfe, J.A. 1972. An interpretation of Alaskan Tertiary floras. Pp. 201–233 in A. Graham (ed.). Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, Amsterdam.
- Wolfe, J.A. 1977. Paleogene floras from the Gulf of Alaska Region. *Geological Survey Professional Paper* 997:1–108.
- Wolfe, J.A. 1979. Temperature parameters of humid to mesic forest of Eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. *United States Geological Survey Professional Paper* 1106:1–37.
- Wolfe, J.A. and H.E. Schorn. 1990. Taxonomic revision of the Spermatopsida of the Oligocene Creed Flora, Southern Colorado. *United States Geological Survey Bulletin* 1923:1–40.
- Wolfe, J.A. and T. Tanai. 1980. The Miocene Seldovia Point Flora from the Kenai Group, Alaska. *United States Geological Survey Professional Paper* 1105:1–52.
- Wolfe, J.A. and T. Tanai. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of Western North America. *Journal of the Faculty of Sciences, Hokkaido University, Series IV* 22:1–246.
- Wolfe, J.A. and W. Wehr. 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. *United States Geological Survey Bulletin* 1597:1–25.
- Worobiec, G. 2003. New fossil flora from the Neogene deposits in the Belchatów lignite mine. *Acta Palaeobotanical, Supplement* 3:3–133.
- Yi, T., A.J. Miller and J. Wen. 2004. Phylogenetic and biogeographic diversification of *Rhus* (Anacardiaceae) in the Northern Hemisphere. *Molecular and Phylogenetics and Evolution* 33:861–879.
- Ying, T.-S., Y.-L. Zhang and D.E. Boufford. 1993. The endemic genera of seed plants of China. Science Press, Beijing. 824 pp.
- Yu, C.-C. and K.-F. Chung. 2017. Why *Mahonia*? Molecular recircumscription of *Berberis* s.l., with the description of two new genera, *Alloberberis* and *Moranothamnus*. *Taxon* 66(6):1371–1392.
- Zuloaga, F.O., R.P. Ellis and O. Morrone. 1993. A revision of *Panicum* Subg. *Dichantherium* Sect. *Dichantherium* (Poaceae: Panicoideae: Paniceae) in Mesoamerica, the West Indies, and South America. *Annals of the Missouri Botanical Garden* 80(1):119–190.

## APPENDIX 1. Extant material used in comparisons.

Species	Collector	Collector no.	Location	Collection date	Specimen no.	Notes
<i>Ailanthus altissima</i> (Miller) Swingle	T.A. Lott		United States: Florida	5/13/2019	UF 6832	
<i>Alnus oblongifolia</i> Torr.	Harde Le Sueur	1304	Mexico: Chihuahua	6/22/1937	UF 4100	
<i>Amelanchier laevis</i> Wiegand	Mark Whitten	5329	United States: Massachusetts	7/6/2016	FLAS 265668	Det. Mark Whitten
<i>Banisteriopsis caapi</i> (Soruca) Morton	R.A. & E.S. Howard	20847	United States: Florida	1/15/1992	FLAS 184538	
<i>Banisteriopsis pubipetala</i> (Adr. Juss.) Cuatr.	Ferreira	9744	Brazil: Obidos	12/4/1987	FLAS 173935	
<i>Castanea pumila</i> (L.) Mill.	V. Call	1548	United States: Florida		UF1548	
<i>Cedrela sinensis</i> A. Juss.	D.L. Dilcher		United States: Pennsylvania	11/5/1974	UF 2356	
<i>Decodon verticillatus</i> (L.) Ell.	M.W. Morris	3323	United States: Georgia	9/24/1988	FLAS 183950	
<i>Dioscorea bulbifera</i> L.	D.L. Dilcher		United States: Florida	May 2005	UF 6173	Det. T.A. Lott
<i>Dipteronia dyeriana</i> A. Henry	A. Henry	11352	China		NYBG 00337738	
<i>Dipteronia sinensis</i> Oliv.	J. Richard Abbott	25906	United States: Tennessee	9/22/2011	FLAS 236695	
<i>Elattostachys verrucosa</i> (Blume) Radlk.					Wing 760	Leaf clearing
<i>Gymnocladus dioica</i> (L.) Koch.	R. Dale Thomas	19971	United States: Arkansas	7/14/1970	FLAS 109207	
<i>Heteropterys brachiata</i> (L.) DC.	Frank	734	United States: Florida	6/26/2005	FLAS 266858	
<i>Heteropterys laurifolia</i> (L.) A. Juss.	Menninger		United States: Florida	1/11/1954	FLAS 66336	
<i>Heteropterys macradena</i> (DC.) W.R. Anderson	Miller & Hauk	9332	Suriname: Sipaliwini	2/4/1998	FLAS 240221	
<i>Heteropterys nervosa</i> A. Juss.	McDoniel et al.	32865	Peru: Loreto	3/15/1995	FLAS 192280	
<i>Heteropterys purpurea</i> (L.) Kunth	Ahles	70611	Puerto Rico	3/31/1968	FLAS 230858	
<i>Heteropterys subhelicina</i> vel sp. Aff. Nied.	Evans et al.	3377	Surinam: Sipaliwini	6/1/2003	FLAS 240222	
<i>Heteropterys syringifolia</i> Gris.	Howard	1948	United States: Florida	11/7/1945	FLAS 43495	
<i>Humulus lupulus</i> var. <i>lupuloides</i> E. Small	W.C. Brumbach	739.32	United States: Pennsylvania	9/22/1932	FLAS 130057	Det. W.C.B.
<i>Hydrangea arborescens</i> L.	J. Richard Abbott	25824	United States: Illinois	10/4/2010	FLAS 236133	
<i>Koelreuteria elegans</i> (Seem.) A.C.Sm.	L.E. Urbatsch		United States: Louisiana	9/15/1976	FLAS 127929	
<i>Koelreuteria paniculata</i> Laxm.	J. Richard Abbott	20827	United States: Missouri	5/4/2006	FLAS 221302	

## APPENDIX 1 (cont.). Extant material used in comparisons.

Species	Collector	Collector no.	Location	Collection date	Specimen no.	Notes
<i>Leucaena leucocephala</i> (Lamarck) de Wit	S.F. Brockington	39	United States: Florida	10/6/2002	FLAS 220373	Det. S.F. Brockington
<i>Macroptilium lathyroides</i> (L.) Urban	Taylor S. Sprenkle	239	United States: Florida	12/14/2003	FLAS 214393	Det. Taylor S. Sprenkle
<i>Nekemias arborea</i> (L.) J. Wen & Boggan	T.A. Lott		United States: Florida	5/9/2019	UF 6831	
<i>Ostrya virginiana</i> (Mill.) K. Koch	S.R. Manchester		United States: Florida	August 1986	UF 4104	Det. S.R. Manchester
<i>Paliurus ramosissimus</i> (Lour.) Poir.	Dilcher & Kokouja		Japan		UF 0987	
<i>Peltophorum pterocarpum</i> (DC.) Back	Erdman West		United States: Florida	9/8/1947	FLAS 47478	Det. Beckner 1968
<i>Platanus occidentalis</i> L.	T.A. Lott		United States: Florida	7/7/2005	UF 5843	
<i>Pinus bungeana</i> Zucc. ex Endl.			United States, Washington, DC		UF 0917	
<i>Pinus elliotii</i> Engelm.	D.L. Dilcher		United States: Florida	September 1998	UF 0990	
<i>Quercus hemispherica</i> Bartr. ex Willd.	Ann George	36	United States: Florida	8/18/2004	FLAS 218616	
<i>Quercus laurifolia</i> Michx.	Cathleen Kabat	535	United States: Florida	6/2/2002	FLAS 210970	Det. C. Kabat
<i>Quercus mohriana</i> Buckl.	Muller	8667	United States: Texas	1945	UF 3156	
<i>Quercus elliptica</i> Nee	C.H. Muller	1951	Mexico: Oaxaca	March 1939	UF 645	
<i>Rhus copallinum</i> L.	M. Whitten	4269	United States: Alabama	6/30/2015	FLAS244300	
<i>Rhus glabra</i> L.	T.A. Lott		United States: Florida	5/18/2001	UF 6323	
<i>Ribes amarum</i> McClat.	D.F. Howe		United States: California	3/8/1970	FLAS 114384	
<i>Ribes sativum</i> Syme	W.C. Muenscher		United States: New York	5/20/1950	FLAS 79595	
<i>Styrax americanus</i> Lam	K.A. Heuberger	57	United States: Florida	4/19/1997	FLAS 205528	
<i>Talguenea quinquenervia</i> I.M. Johnst.	Otto Zollner	9042	Chile	10/5/1975	UF 3042	
<i>Toxicodendron radicans</i> (L.) Kuntz	T.A. Lott & A. Lott		United States: Florida	9/3/2000	UF 1010	
<i>Toxicodendron radicans</i> (L.) Kuntz	S. Barry Davis	681	United States: Florida	3/31/2003	FLAS 211507	
<i>Wisteria sinensis</i> (Sims) Sweet	Mark Whitten	4095	United States: Florida	10/22/2014	FLAS 242130	
<i>Zizyphus inermis</i> Merrill	M. Ramos	1960	Phillipines: Luzon	November 1914	UF 2413	

**APPENDIX 2:** Leaf data for foliar physiognomy estimates of MAT and MAP.

**Leaf Margin Analysis**

Species	Margin	Avg. Leaf area mm <sup>2</sup>
<i>Laurophyllum eocenicum</i>	E	896.8
<i>Daphnogene knowltonii</i>	E	764
<i>Mahonia simplex</i>	S*	1002.6
<i>Mahonia</i> sp. 2	S*	853
<i>Platanus exaspera</i>	S	3144.8
cf. <i>Parrotia</i>	S	252
<i>Ribes</i> sp.	S	1625
Morphotype TRL04	S	1429
<i>Cercis parvifolia</i>	E	793
cf. <i>Gymnocladus dayana</i>	E	928.2
cf. <i>Gymnocladus hesperia</i>	E	963.8
Morphotype TRL 05	E	158.1
Morphotype TRL 06	E	372.5
Morphotype TRL 07	E	71
<i>Amelanchier</i> sp	S	908.5
cf. <i>Crataegus</i>	S	138.5
<i>Cedrelospermum</i> sp.	S	140
<i>Ulmus chuchuanus</i>	S	606.5
<i>Ulmus okanaganensis</i>	S	775.1
<i>Alnus newberryi</i>	S	1960
<i>Carpinus/Ostrya</i>	S	316.8
cf <i>Carpinus</i>	S	N.A.
<i>Quercus berryi</i>	S	441.1
<i>Quercus pollardiana</i>	E	426.5
<i>Quercus</i> sp. 1	E	192.3
<i>Quercus</i> sp. 2	S	377
<i>Juglandiphyllites cryptatus</i>	S	625.3
<i>Decodon</i> sp.	E	409.7
<i>Rhus lesquereuxii</i>	S	1631.8
cf. <i>Toxicodendron</i>	E	493.5
<i>Acer clarnoense</i>	S	1242.7
<i>Acer</i> sp. 1	S	961.6
cf. <i>Elattostachys</i>	S	2118
cf. <i>Ailanthus</i>	S	1178.5
<i>Plafkeria</i> sp.	E	1369.8
<i>Flectorivus</i> sp.	S	213.5
Morphotype TRL 10	E	349

Species	Margin	Avg. Leaf area mm <sup>2</sup>
Morphotype TRL 11	S	371
Morphotype TRL 12	S	575
Morphotype TRL 13	S	905
<b># Morphotypes</b>	<b>40</b>	<b>39</b>
<b># untoothed</b>	<b>14</b>	
<b>% entire</b>	<b>35</b>	

\*the spiny teeth of *Mahonia* are treated as “no teeth” in protocol for CLAMP, but are scored as teeth present for leaf margin analyses.