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Loxopteroides weeksae gen. et sp. nov. (Anacardiaceae) samaras and associated foliage from the Eocene of western North America

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ABSTRACT. An extinct kind of winged fruit found at several Eocene sites in California and Oregon, western USA, occurs in association with pinnately compound anacardiaceous leaves that have been called *Rhus mixta*. The samaras were previously treated along with isolated leaves from the Chalk Bluffs flora of California in an extinct sapindaceous genus, *Thouiniopsis myricaefolia* (Lesquereux) MacGinitie. However, the samaras are non-schizocarpic and hence readily distinguished from the mericarps of extant Sapindaceae such as *Acer*, *Thouinia* and *Thouinidium*. We reassign the fruits to Anacardiaceae and note similarity to the extant Neotropical genus *Loxopterygium* which differs, however, in the shape of the endocarp and placement of the style. Fruits of *Loxopteroides weeksae* gen. et sp. nov. co-occur with leaves of *Rhus mixta* at multiple localities in California and Oregon.

KEYWORDS: fossil, leaves, fruits, *Loxopterygium*, Chalk Bluffs, California, Clarno Formation, Oregon

INTRODUCTION

The Anacardiaceae are a widespread angiosperm family distributed in temperate to tropical regions with about 80 extant genera and 800 species (Pell et al., 2011). Some of the modern genera, including *Rhus* and *Anacardium* have been traced with confidence back to the Eocene based on distinctive fruit characters (Manchester, 1994; Manchester et al., 2007, respectively). Fruits in the family commonly are drupes, but some genera are characterized by conspicuously winged fruits. The drupaceous fruits of subfamily Spondioideae have distinctive endocarp morphology – characterized by one to several single-seeded locules each with a germination pore and/or valve – that allows their recognition in the fossil record (Herrera et al., 2018). The fossil record of winged anacardiaceous fruits is less well known but includes *Loxopterygium* samaras in the Miocene of Ecuador (Burnham and Carranco, 2004).

Winged fruits occur in several extant genera of the Anacardiaceae, all in the subfamily Anacardioideae (Pell et al., 2011). Some have accrescent perianth forming a propeller-like dispersal unit, e.g. *Astronium*, *Gluta*, *Loxostylus*, *Myracrodruon* and *Swintonia*. Others have paired wings developed from the ovary (*Cardenasiodendron*, *Pseudosmodingium*), or a single surrounding wing (*Smodingium*). Fruits with a single extended wing occur in *Amphipterygium*, *Faguetia*, *Loxopterygium*, *Orthopterygium* and *Schinopsis*.

MacGinitie (1941) identified a small samaroid fruit to the extinct genus and species that he named *Thouinopsis myricaefolia* (Lesquereux) MacGinitie based on foliage from the Eocene Chalk Bluffs flora [*Rhus myricaefolia* Lesquereux, Harvard Mus. Comp. Zool., Mem., vol. 6, no. 2, p. 51, pl. 1, figs 5–7, 1878]. He assigned it

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to Sapindaceae and noted similarities to extant *Thouinia* (Pl. 1A–C) and *Thouinidium* (Pl. 1D). However, the fruits differ from those of Sapindaceae in being non-schizocarpic, and they commonly occur in association with fossil anacardiaceous foliage "*Rhus*" *mixta* Lesquereux.

Here, we provide a new generic name, *Loxopteroides*, for this extinct genus of fruits, because the name *Thouiniopsis* MacGinitie was based upon fossil leaflets and there is no convincing evidence that the fruits and foliage were borne by the same species or genus of plant. In this paper, we describe the fruits in comparison with extant anacardiaceous fruits and review the associated foliage, "*Rhus*" *mixta* from the Eocene of California and Oregon, which we suggest was produced by the same plant.

MATERIALS AND METHODS

The fruits and foliage treated here were collected from the Chalk Bluffs flora of the Ione Formation of the Sierra Nevada, California in historical exposures from hydraulic gold mining (Lesquereux, 1878; MacGinitie, 1941) and from natural shale outcrops of the Clarno Formation in northcentral Oregon (Fig. 1). Specimens of the Chalk Bluffs flora (Lesquereux, 1878; MacGinitie, 1941) were studied at the Museum of Paleontology, University of California, Berkeley (UCMP) and at the Smithsonian Natural History Museum, Washington, DC (USNM), with particular attention to the pink impressions of fruits and foliage from the locality at You Bet, California (MacGinitie, 1941). Those from the Clarno Formation of Oregon were collected near West Branch Creek in Wheeler County and near Cherry Creek in Jefferson County and deposited at the Florida Museum of Natural History, University of Florida, Gainesville, Florida (UF). Specific localities collected by Manchester and teams of students from the Oregon Museum of Science and Industry summer paleobotany programs, including White Cliffs Jr (UF locality 263), White Cliffs Sr (UF 262), Red Gap (UF 251A), John Day Gulch west (UF 236), and West Branch Creek (UF 229, 230) are listed in Table 1.

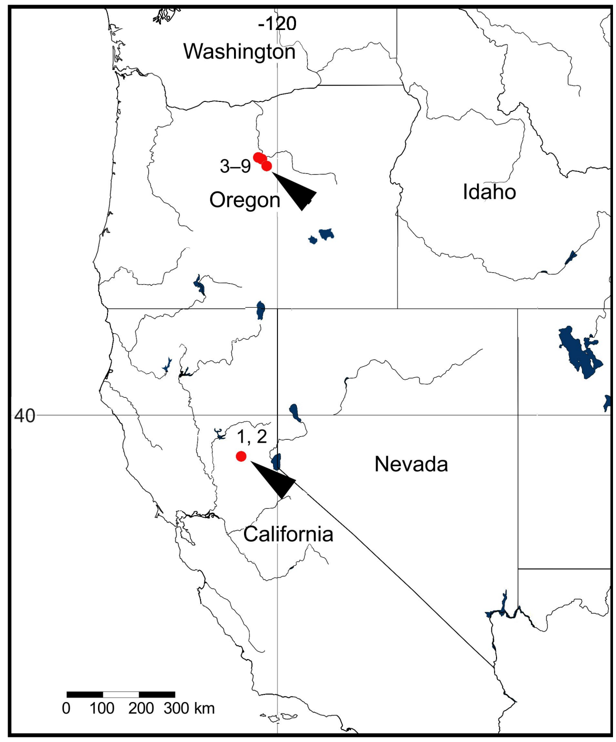

Figure 1. Map showing localities of the Ione (southern arrow) and Clarno (northern arrow) formations from which fruits of *Loxopteroides weeksae* and "*Rhus*" *mixta* were collected. Locality numbers correspond to those indicated in Table 1

The Chalk Bluffs flora of the Ione Formation is considered late early Eocene, ~49–52 Ma, based on stratigraphic correlations with marine units (Wolfe, 1981; Wolfe et al., 1998). The lacustrine shale sites in the Clarno Formation that have yielded the fruits

Table 1. Localities with co-occurrence of "*Rhus*" *mixta* and *Loxopteroides weeksae* (+ = present, NC = not confirmed)

No	Locality	Institutional number	Latitude, Longitude	"*Rhus*" *mixta* leaves	*Loxopteroides weeksae* fruits
1	You Bet, Nevada Co., California	UCMP loc.	39.209170°N, 120.898889°W	+	+
2	Independence Hill, Placer Co., California	UCMP loc.	39.117141°N, 120.849401°W	+	NC
3	Alex Canyon, Wheeler Co., Oregon	UF 229	44.5815000°N, 120.2659194°W	+	+
4	West Branch Cr., Wheeler Co., Oregon	UF230, UCMP 3900	44.5903639°N, 120.2577306°W	+	+
5	White Cliffs Sr, Jefferson Co., Oregon	UF 262	44.7383667°N, 120.4729333°W	+	+
6	White Cliffs Jr, Jefferson Co., Oregon	UF 263	44.7372667°N, 120.473500°W	+	+
7	Gosner Rd, Jefferson Co., Oregon	UF 238	44.7310167°N, 120.4599000°W	+	+
8	Red Gap, Jefferson Co., Oregon	UF 251A	44.7387333°N, 120.4158833°W	+	+
9	John Day Gulch west, Wheeler Co., Oregon	UF 236	44.7072333°N, 120.3850500°W	+	+

and foliage treated here are middle Eocene based on plagioclase K-Ar dates of 46.78 ±1.45 Ma and 46.78 ±1.45 Ma at the White Cliffs and Red Gap localities, respectively (Manchester, 1990). Although not radiometrically constrained, the West Branch Creek shales are probably similar in age based on florisitic similarities with the White Cliffs flora. The lacustrine shales of the John Day Gulch locality of the Clarno Formation have been inferred to be late Eocene, ~40 Ma, based on stratigraphic position and floristic and physiognomic characteristics (Wolfe, 1992; Manchester, 2000).

Fossil specimens and extant comparative material were photographed with a Canon XSI digital camera fitted with a Canon 60 or 100 mm macro lens, and for higher magnifications using a Zeiss Luminar 63 mm lens with diffuse low-angle tungsten lighting. Fruits of extant *Loxopterygium* and other genera were studied at herbaria of UC, MO, and photographed with the same apparatus. Micro-CT scanning was performed at the Nanoscale Research Facility, College of Engineering, University of Florida with a GE Phoenix V|tome|xm240 CT scanner. For modern fruits we used a voltage of 90 kV and current of 250 µA producing scans with 2000 projections at 0.333 s each and a voxel size resolution of 28 µm. For fossil fruits in siltstone, we used a voltage of 188 kV and current of 250 µA producing scans with 2200 projections at 0.2 s each and a voxel size resolution of 42 µm. Datasets reconstructed as Tiff stacks from the µ-CT scans were analyzed with Avizo v.9.0 Lite (FEI Visualization Science Group, Bordeaux, France) and VG Studio Max v.3.1 (Volume Graphics, Inc., Heidelberg, Germany) to generate volume and surface renderings, and to produce isosurface renderings that were exported as Stanford .ply files and examined with MeshLab (http://www.meshlab.net/). The depth map rendering option in MeshLab was especially useful for displaying surface topography for images presented herein.

RESULTS

SYSTEMATIC PALAEOBOTANY

Order SAPINDALES
Juss. ex Bercht. et J. Presl, 1820

Family ANACARDIACEAE R. Br., 1818

Genus ***Loxopteroides***
Manchester et Judd **gen. nov.**

Etymology. The generic name refers to the oblique orientation of the wing on these fruits and the similarity of these samaras to those of extant *Loxopterygium*.

Type species. *Loxopteroides weeksae* Manchester et Judd, sp. nov.

Generic diagnosis. Fruit an asymmetrically winged samara about 2.5 times longer than wide, pedicellate with a hypogynous perianth scar at junction of pedicel with the fruit body. Pedicel thin. Samara with a laterally flattened elliptical endocarp, with 12–16 longitudinal ribs that are oriented obliquely, at an angle of 30–40° to the long axis of the samara. Wing with elongate, arching subparallel veins extending to the lower and distal margins of the wing. Veins mostly of one order, with some anastomosing and dichotomizing, 2.6 veins per mm, more densely spaced along the upper margin than along the lower and distal margins. A fine fimbrial vein defines periphery of the wing.

Loxopteroides weeksae
Manchester et Judd, **sp. nov.**

Pl. 1A–O

Holotype. Designated here: USNM PAL 772318.

Paratypes. USNM PAL 772319-772322.

Repository. Smithsonian Natural History Museum, Washington, DC (USNM).

Type locality and stratigraphic horizon. You Bet, California (Ione Formation).

Additional specimens studied. UCMP 2291 (You Bet, California), UF 229-19484 (Alex Canyon, Oregon), UF 230-18276, 18279, 18280, 18285, 18286, 18287, 18292 (West Branch Creek, Oregon), UF 263-16886, 16889 (White Cliffs Jr., Oregon), UF 262-17781, 17782, 17783 (White Cliffs Sr., Oregon), 238-19952 (Gosner Road, Oregon), UF 236-84783 (John Day Gulch west, Oregon).

Etymology. The epithet recognizes Dr. Andrea Weeks for her contributions to systematic botany and our understanding phylogeny of the Sapindales.

Diagnosis. Same as for genus.

Nomenclature. These fruits were formerly attributed to the extinct genus and species, *Thouinopsis myricaefolia* (Lesquereux) MacGinitie (MacGinitie, 1941: p. 142, pl. 37, fig. 6). However, that species was found by Lesquereux (1878) on foliage alone [*Rhus myricaefolia* Lesq.]. As both leaves and fruits were found together in the Chalk Bluffs flora, MacGinitie proposed they were from the same plant and were referable to the Sapindaceae. We, however, doubt that these organs were produced by the same plant because such leaves are not found in association with the samaras at sites in the Clarno Formation. It is more likely that the fruits can be linked with the anacardiaceous foliage commonly referred to as *Rhus mixta* Lesquereux, which occurs in both the Chalk Bluffs and Clarno floras. In any case, lacking physical attachment to prove the connection between fruits and foliage, we consider it appropriate to name a genus to accommodate the isolated fruits.

Description. Asymmetrically winged samara, 7.2–9.8 mm long, 2.9–4.0 mm wide, about 2.5 times longer than wide, with thickened scar of hypogynous perianth. Pedicel thin (0.1–0.2 mm) and short (0.5 mm) (Pl. 1A–G, M). Endocarp elliptical, laterally flattened 1.5–2.0 mm wide, 2.2–3.0 long, with prominent longitudinal ribs, about 6–8 ribs over each lateral surface (Pl. 1M–O), collectively 12–16 ribs on both sides, oriented obliquely, at an angle of 30–40° to the long axis of the samara (Pl. 1A–O). Wing with elongate, somewhat arching subparallel veins extending to the lower and distal margins of the wing. Veins mostly of one order, with some anastomosing and dichotomizing, 2.6 veins per mm, more densely spaced along the upper margin than along the lower and distal margins. A fine fimbrial vein extends along the periphery of the wing (Pl. 1D, E, J, L, M). Style or style remnant indistinct.

Systematic position. We compared these samaras with those of various extant families, including those with asymmetrical samaras reviewed by Mirle and Burnham (1999). As MacGinitie (1941) recognized, somewhat similar samaras occur in Sapindaceae, e.g. *Acer*, *Serjania*, *Thinouia* (see Pl. 2A–C), and *Thouinidium* (Pl. 2D), but these are schizocarpic fruits that disperse as mericarps with a clear scar of detachment from the adjoining mericarps. The samaras of Rutaceae (*Helietta*) and Malphighiaceae (e.g., *Banisteria*, *Heteropterys*) are also schizocarpic. We conclude that the fossil was not schizocarpic because the fruits have a pedicel and perianth scar intact beneath just one endocarp (Pl. 1A, C, D, J, L–O), and they lack a distinct lateral scar that would indicate detachment from adjoining mericarps.

Some fruits of Leguminosae have asymmetrical samaras (e.g. Jia et al., 2017; Martínez, 2018), but they are usually stipitate, and typically are smooth, rather than ribbed, over the endocarp body and have a terminal style. Other taxa with samaroid fruits that can be excluded belong to Malvaceae (e.g. *Mansonia*, *Tarrietia*, *Triplochiton*, all with significantly larger fruits), Petiveriaceae (*Gallesia* [Pl. 2E], *Seguieria* [Pl. 2F]), Ulmaceae (*Cedrelospermum*, *Phyllostylon*) and Celastraceae (*Zinowiewa*).

Loxopterygium of the Anacardiaceae has fruits similar in size and shape to our fossil (Pl. 2I, J). Both have a longitudinally coarsely ribbed fruit body and a thin pedicel which widens at junction with the hypogynous perianth at junction with base of the fruit (Pls 1M, 2H, K). They are also similar in wing shape and venation. Notable differences are that in *Loxopterygium* the persistent style remnant is displaced distally on the wing (Pl. 2H, I, K), and the endocarp is more elongate (about 3 times longer than wide, e.g. Pl. 2K) compared to that in *Loxopteroides* (1.2–1.5 times longer than wide, Pl. 1A–O).

"*Rhus*" *mixta* Lesquereux

Pls 3A–F, 5A, C, D

Basionym. *Rhus mixta* Lesquereux, 1878, Harvard Coll, Mus. Comp. Zool, Mem, vol. 6, no. 2, 30, pl. 9, fig. 13, lone Gravels: Chalk Bluffs, Nevada Co., California; MacGinitie, 1941, Carnegie Inst. Washington Pub. 534, 142, pl. 35, figs 1, 4; pl. 36, fig. 1, Ione Gravels: Placer and Nevada Co., California.

Synonymy.

1946 *Koelreuteria mixta* (Lesquereux) Brown, Washington Acad. Sciences, Jour, vol. 36, 351, text-f. 1, 2.

Emended description. Leaves odd-pinnately compound with 11 or more leaflets (Pls 3A, D, 4A, D). Rachis up to at least 7 cm long (Pl. 4D). Leaflets petiolulate (Pls 3B, F) to nearly sessile (Pls 3A, D, 4A, D), ovate, asymmetrical, with acute base and apex, usually prominently serrate, 1.1–8.5 cm long, 0.3–2.8 cm wide, length/width ratio 3.1 to 4.6. Venation pinnate with 7–18 pairs of slightly curved, craspedodromous to cladodromous secondary veins. Some secondary veins leading directly to marginal teeth, others entering a marginal sinus, still others entering entire portion of the margin. Secondary veins typically enter the teeth submedially. Intersecondary veins common (Pls 3E, F, 4C). Tertiary veins percurrent alternate typically oriented nearly perpendicular to the

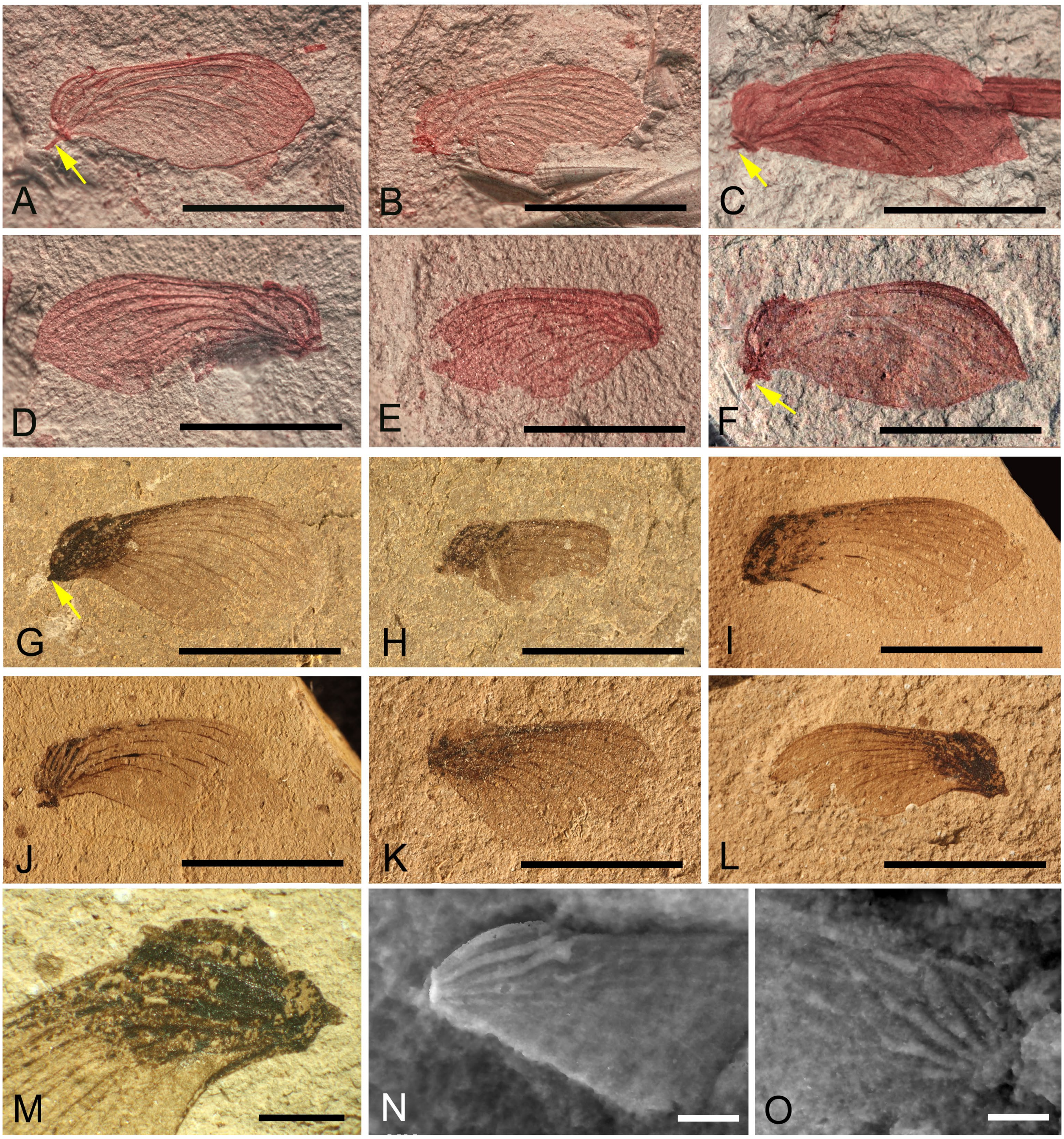

Plate 1. *Loxopteroides weeksae* samaras from the Eocene of California and Oregon. **A–F**. Specimens from You Bet, California, by reflected light, with arrows indicating narrow pedicel below the hypogynous perianth scar. **A**. Holotype, USNM PAL 772318; **B**. USNM PAL 772319; **C**. USNM PAL 772320; **D**. USNM PAL 772321; **E**. USNM PAL 772322; **F**. UCMP P-2291 (Orig. fig. MacGinitie 1941); **G–M**. Specimens from the Eocene Clarno Formation of Oregon by reflected light. **G**. UF 230-18287, specimen with the thin pedicel intact (arrow), West Branch Creek; **H**. 18285, West Branch Creek; **I**. UF 263-16886, White Cliffs Jr.; **J**. UF 262-17781, White Cliffs Sr.; **K**. UF 230-18285, West Branch Creek; **L**. UF 263-16889, White Cliffs Jr.; **M**. Enlargement from L, showing prominent thickening at base of fruit with scar of perianth and disk. **N–O**. Surface ribbing of endocarp viewed by depth map of surface rendering from micro-CT scan; **N**. UF 262-17782; **O**. UF 262-17783. Scale bars 5 mm in A–L, 2 mm in M, 1 mm in N, O

midvein, often weakening midway between secondary veins. Teeth simple. Tooth apices acute, sharp to rounded, but not spiny or glandular, sinuses angular.

Type locality and stratigraphic horizon. Independence Hill, Placer Co., California (Ione Formation).

Other localities. You Bet, California (Ione Formation); White Cliffs (UF 263, 263), Red Gap, Gosner Road, West Branch Creek, John Day Gulch, Oregon (Clarno Formation).

Specimens studied. UF 262-17604, 263-17445, 17537, 17556, 35488 (White Cliffs), UF 230-18603 229c-47128 (West Branch Creek),

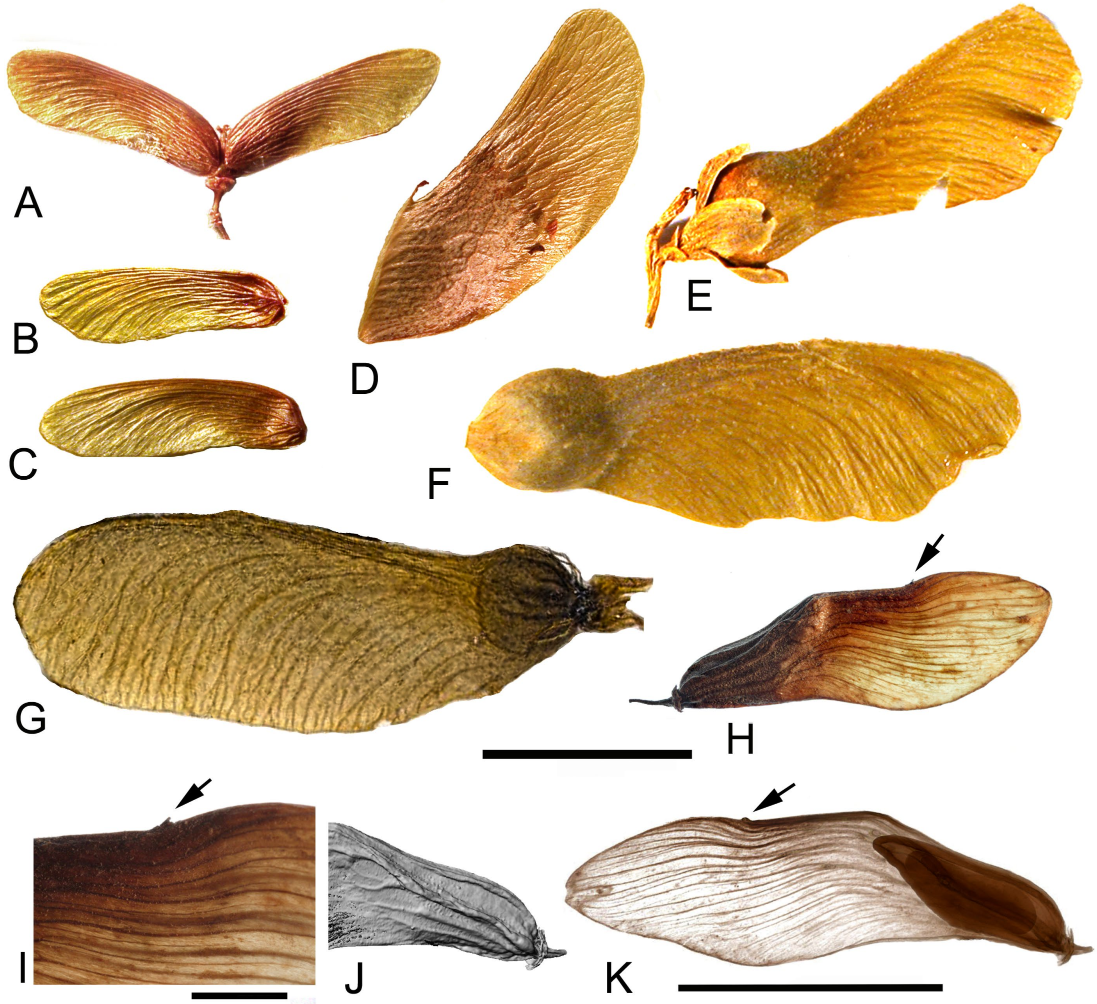

Plate 2. Extant fruits for comparison. **A–C**. Sapindaceae: *Thouinia acuminata* Watson Jalisca, Mexico, NY: C.G. Pringle 2485. **A**. Schizocarp with both mericarps still attached; **B**, **C**. Isolated mericarps. Note that pedicel and perianth do not disperse with the fruit, contrary to *Loxopteroides*; **D**. Sapindaceae: *Thouinidium inequaelaterum* Alain mericarp, Dominican Republic NY: H.A. Liogier 18114; **E**, **F**. Petiveriaceae: *Gallesia integrifolia* (Spreng.) Harms. Brazil, MO: Krukoff 5405 (BARC); **G**. Petiveriaceae: *Seguieria langsdorfii* Moq. ASU 44305: G. Hatschbach and J. Cordeiro 52684 Minas Gerais, Brazil; **H–K**. Anacardiaceae: *Loxopterygium grisebachii* MO 6077207: Nee & Flores 54865, Bolivia, with arrow indicating position of style on wing margin; **H**, **I**. Transmitted plus reflected light I, J, showing narrow pedicel, persistent perianth; **J**, **K**. Surface view, and volume rendering from micro-CT scan. Scale bars = 1 cm in A–H, K (bar in H applies to A–G, bar in K applies also to J; 2 mm in I

UF 236-84783, 84784, 84785 (John Day Gulch). UF 238-19864, 20063 (Gosner Road); UF 242-19668 (Horse Heaven); UF 251A-46859, 46983, 52669 (Red Gap).

Comments. This foliage type was initially described as *Rhus mixta* by Lesquereux (1878) and the identification was accepted by MacGinitie (1941). Brown (1946) transferred the species to *Koelreuteria*, but we do not accept that transfer because the leaflets show a weakening of tertiary veins midway between successive secondary veins (well seen in Pl. 3E) a feature characteristic of some Anacardiaceae (Ramírez and Cevallos-Ferriz, 2002; Martínez-Millán and Cevallos-Ferriz, 2005) including *Astronium*, *Loxopterygium*, *Rhus* and *Toxicodendron*, but absent from *Koelreuteria* and other Sapindaceae. Despite the close similarity of the fossil foliage to extant *Rhus* leaves, we have not found the distinctive impressions of *Rhus* fruits in co-occurrence. Because *Rhus*-like foliage is found in more than one genus of the Anacardiaceae today, it is difficult to confirm that *R. mixta* belongs to the genus *Rhus*. Because of its shared provenance with the fruits of *Loxopteroides* at You Bet, California, and seven localities in Oregon (Tab. 1), we suggest that this foliage belonged to the same plant that produced the *Loxopteroides* samaras. Lacking direct evidence from physical attachment, this remains unproven; therefore we refrain from a formal nomenclatural merger of these

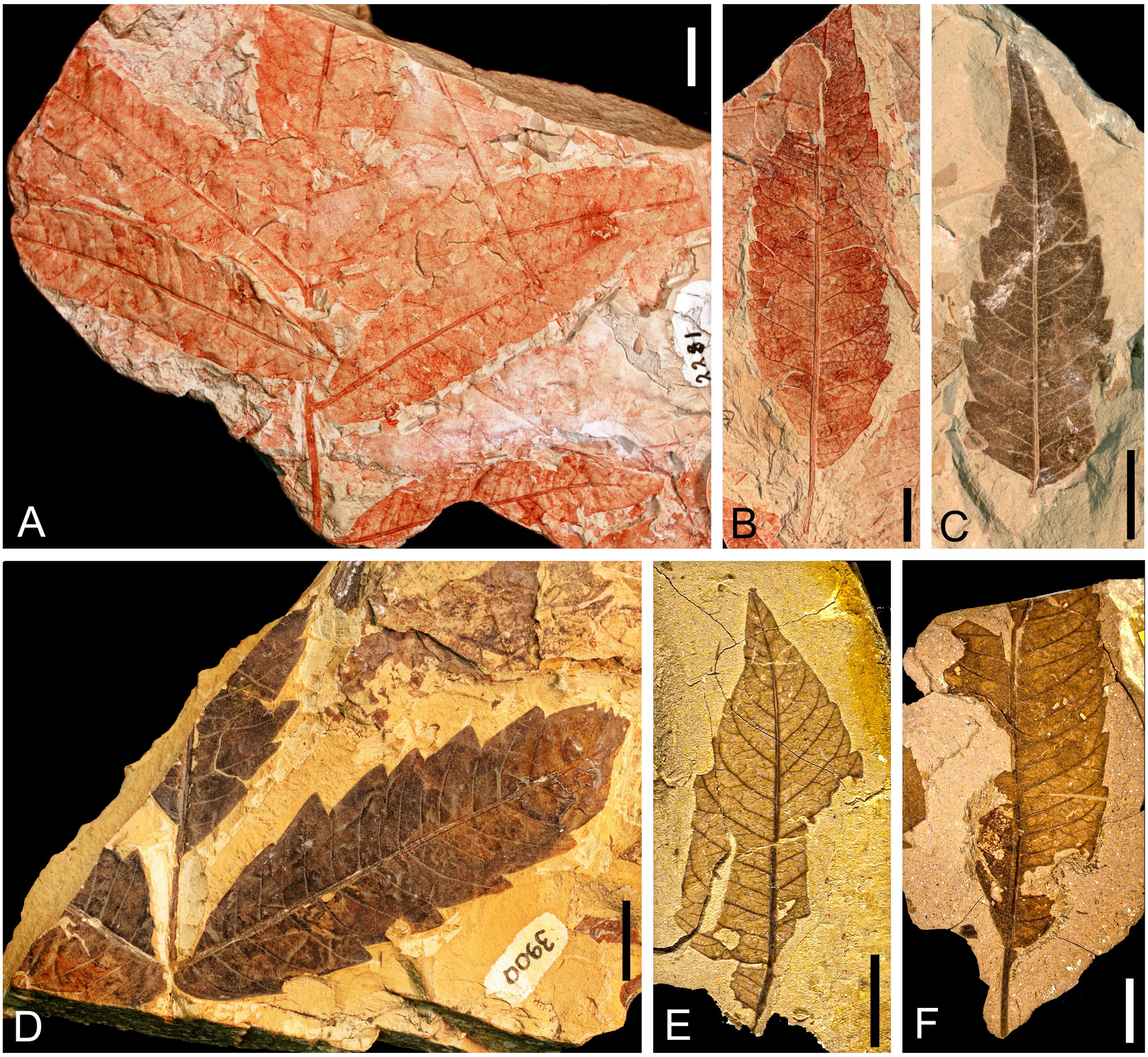

Plate 3. "*Rhus*" *mixta* foliage from the Eocene of California and Oregon. **A–C**. Ione Formation, California. **A**. Portion of imparapinnately compound leaf showing at least seven leaflets (lower left inferred from symmetry), UCMP 2281; **B**. Isolated petiolulate leaflet, UCMP 2280; **C**. Leaflet, UCMP 2279; **D–F**. Clarno Formation, Oregon; **D**. Terminal portion of compound leaf, UCMP 254964, UCMP loc. 3900, West Branch Creek, Oregon; **E**. Apical portion of leaflet, White Cliffs Sr, UF 262-17604; **F**. Petiolulate leaflet, White Cliffs Jr, UF 263-17537. Scale bars = 1 cm

taxa. However, we recommend that the foliage assignment to *Rhus* be regarded as tentative; we indicate this by bracketing the generic name with quotation marks: "*Rhus*" *mixta* Lesquereux. The use of quotation marks to indicate questionable generic assignment of a previously published binomial follows the procedure of Hickey (1977). We considered the possibility to erect a new genus for these leaf and leaflet fossils, but were unable to offer a suite of characters for the diagnosis that would exclude leaves of some extant species of *Rhus*. Despite our concern that more than one genus produces *Rhus*-like foliage, most investigators will probably continue to assign such fossils to *Rhus*.

DISCUSSION

Within the phylogeny of Anacardiaceae as presented by Weeks et al. (2014), we can infer that *Loxopteroides* belongs to the subfamily Anacardioideae, as none of the extant or fossil genera of the other subfamily, Spondioideae, possess winged fruits (Herrera et al., 2018). More specifically, *Loxopteroides* likely belongs to a subclade within "Anacardioideae 2" resolved in the phylogeny of Weeks et al. (2014) based on *ETS*, *trnL-F* and *rps16*. This subclade in their analysis accommodates the Neotropical genera *Apterokarpos*, *Astronium*, *Cardenasiodendron*, *Loxopterygium*, *Myracrodruon* and *Schinopsis* (Weeks et al., 2014), which except for

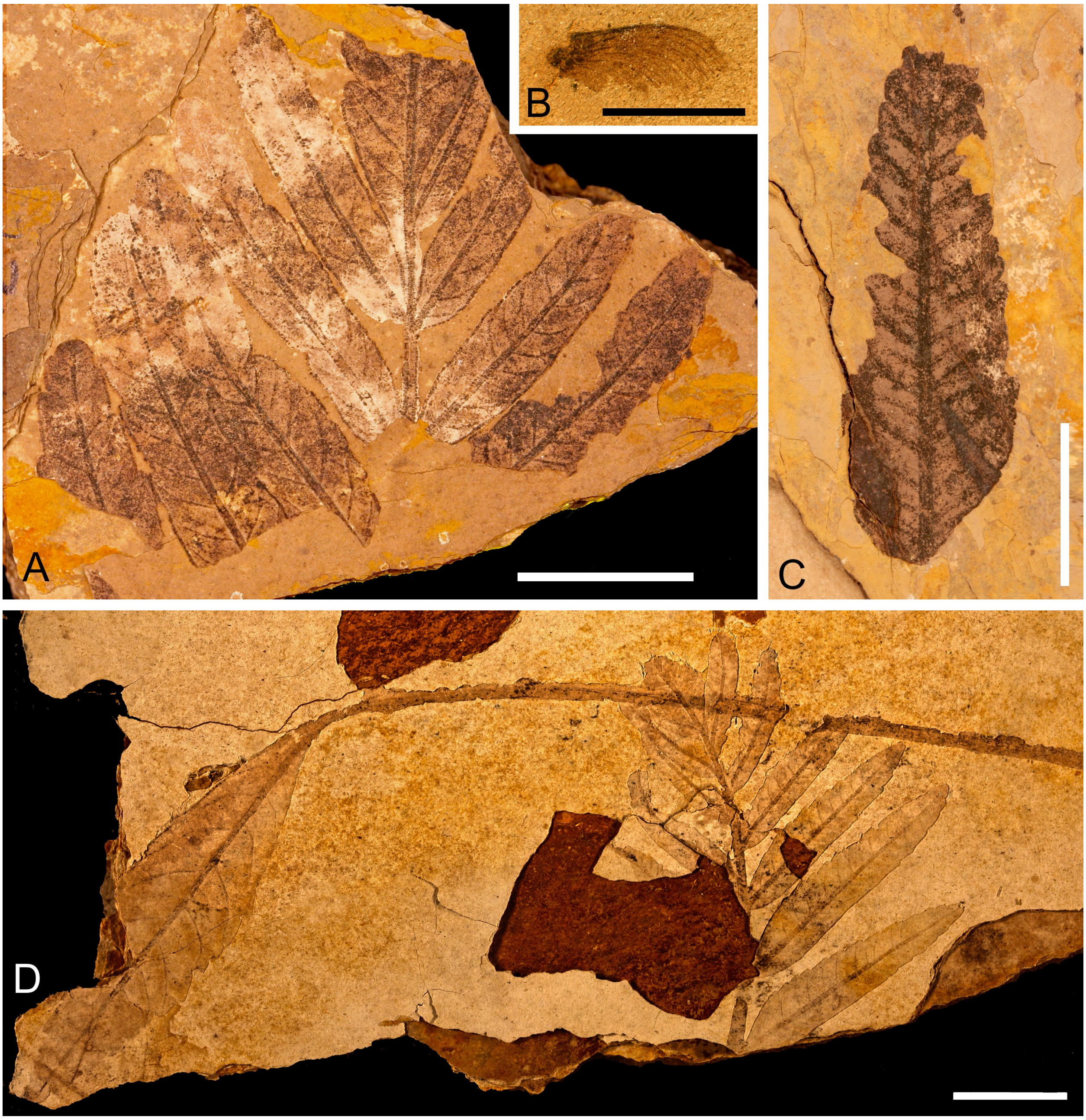

Plate 4. "*Rhus*" *mixta* foliage and *Loxopteroides weeksae* samara from Eocene John Day Gulch west locality, Oregon. **A**. Portion of compound leaf with a terminal leaflet and at least 10 lateral leaflets (some of them inferred from symmetry), UF 236-84783; **B**. Fruit of *L. weeksae*, UF 236-84786; **C**. Isolated leaflet, UF 236-84785; **D**. Paper shale slab bearing a compound leaf with a terminal leaflet and the terminal leaflet of a larger leaf (left side of image) on a rachis with the lateral leaflets shed, UF 236-84784. Scale bars = 1 cm in A, C, D, 5 mm in B

Apterokarpos, have wind-dispersed fruits. The wings in *Astronium* and *Myracrodruon* develop from accrescent perianth, while those of *Cardenasiodendron*, *Loxopterygium* and *Schinopsis* develop from ovary tissue, as in *Loxopteroides*.

Loxopteroides samaras overlap in size with the samaras of another extinct genus, *Barkleya*, from the Eocene Green River Formation of Utah, Colorado and Wyoming (Manchester and Judd, 2022). Those fruits also co-occur with *Rhus*-like foliage, which has been called *Rhus nigricans*. The leaves and leaflets of *R. mixta* and *R. nigricans* are nearly indistinguishable in architecture.

The two genera of samaroid anacardiaceous fruits in the Eocene of western North America, i.e. *Barkleya* from the Rocky Mountain region and *Loxopteroides* from the west coastal region, augment the diversity of winged fruits known to have evolved in this family. As both fruit types occur with foliage that closely resembles that of *Rhus*, we should not assume that all the leaflets of Anacardiaceae recovered from Cenozoic deposits will be referable to extant genera.

Loxopteroides is accompanied by a variety of other winged fruits in the lacustrine floras of the Clarno Formation, including *Ailanthus* (Corbett and Manchester, 2004), *Cedrelospermum* (Manchester, 1987b), *Cruciptera* (Manchester, 1991), *Ulmus* (Manchester, 1989), *Alnus* (Liu et al., 2014), *Engelhardia*, *Hooleya* (Manchester, 1987a), *Dipteronia* (McClain and Manchester, 2001), *Deviacer* (Manchester, 1994), *Chaneya* (Wang and Manchester, 2000), *Illigera* (Manchester and O'Leary, 2010), *Lagokarpos* (McMurran and Manchester, 2010). In the Chalk Bluffs flora MacGinitie (1941) recognized several winged disseminules, including those assigned to *Ulmus*, *Engelhardia*, *Fraxinus*, *Ailanthus*, *Cercidiphyllum*, *Liquidambar* and *Terminalia.* These were part of the spectrum of dispersal types represented, as these floras also included a large proportion of nuts and fleshy fruits adapted for animal dispersal (Manchester, 1994). A fruit of *Ensete* (Musaceae) was recovered from the West Branch Creek shales (Manchester, 1995), and seeds of the same genus have been observed at the John Day Gulch locality, as well as at the Clarno Nut Beds (Manchester and Kress, 1993; Manchester, 1994). These taxa, together with a cycad resembling *Dioonopsis* at West Branch Creek and John Day Gulch, indicate conditions perhaps with relatively warm, mostly frost-free winters, while the presence of *Pinus*, *Sequoia*, and deciduous angiosperms such as Platanaceae, Juglandaceae, Betulaceae and Ulmaceae indicate likely temperate conditions.

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