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Winged fruits of *Pteleoidea* gen. nov. from the Paleocene of Wyoming, USA

ARIANNE A. LOPEZ DEL RINCON[1] and STEVEN R. MANCHESTER[1*]

[1]Florida Museum of Natural History, Dickinson Hall, Gainesville, Florida 32611-7800, USA;
e-mails: arianneldr@gmail.com; steven@ufl.edu, ORCID: 0000-0003-0238-7977

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ABSTRACT. Winged fruits formerly attributed to *Koelreuteria* from the Paleocene Fort Union Formation of southwestern Wyoming are reevaluated. Numerous additional specimens have been collected to supplement the original treatment of *K. annosa* Brown, which was based on only one specimen. Differences from extant and fossil species of *Koelreuteria* lead us to recognize a new genus. *Pteleoidea annosa* (Brown) gen. et comb. nov. is characterized by elliptical fruits with a pair of wings lying in a common plane, with an apical style and borne on a long, narrow pedicel. The fruit possesses a hypogynous nectary disk and perianth. The central fusiform locular region sometimes preserves elongate elliptical seeds, borne in axile attachment. Although the fruits do not conform precisely to an extant genus, sapindalean affinity, possibly with the Rutaceae, is suggested. Gland-dotted serrate leaflets found in association with the fruits are also inferred to be of sapindalean affinity. These remains add to the diversity of extinct eudicots encountered in the Paleocene of North America.

KEYWORDS: extinct angiosperm, Sapindales, *Koelreuteria annosa*, Fort Union Formation

INTRODUCTION

Wind-dispersed fruits take many forms among angiosperms, ranging from laterally winged samaras like those of *Acer* L. 1753 (Mirle and Burnham, 1999), and those with propeller-like wings, such as *Abelia* R.Br. 1818 and *Ruprechtia* C.A.Mey. 1840 (Manchester and Uemura, 2013), to those with radiating lateral wings (‘fin-winged’), such as *Combretum* Leofl. 1758 and *Halesia* P.Browne 1756 (Manchester and O’Leary, 2010). Such fruits can be distinguished from one another by the number of carpels, the position of perianth (epigynous vs hypogynous), the number, form, and venation of wings and details of the seeds within them. The fin-winged fruit type has evolved in many angiosperm lineages (Manchester and O’Leary, 2010).

Here we revisit a fossil species from the Paleocene of Wyoming that was previously attributed to the sapindaceous genus *Koelreuteria* Laxm. 1772. The fossil fruit species *Koelreuteria annosa* R.W. Brown was established based on a single specimen collected near Point of Rocks, Wyoming (Brown, 1956, 1962). Although *Koelreuteria* fruits were confirmed from Eocene and younger sites across the Northern Hemisphere (Wang et al., 2013), Brown’s species is morphologically distinct. Whereas extant *Koelreuteria* fruits are bladder-like capsules that fall into three wing-like valves, the fossils in question have only a single pair of wings spreading in one plane. The identification of the Paleocene fruit as *Koelreuteria* was already questioned (Manchester, 2014), but a revised generic placement was not provided. More specimens from two additional localities provide new data on the morphology of these fruits and help us to identify a set of informative characters helpful to infer the most likely botanical affinities. In addition, we

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[*] Corresponding author

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recognize a new type of fossil foliage at two of the sites where these fruits occur, and infer that those leaves might have been produced by the same species. Here, we describe the fruits as a new genus, *Pteleoidea*, provide a synopsis of the associated foliage, and present our hypothesis of affinity with Rutaceae.

MATERIAL AND METHODS

We examined 51 specimens of the fossil winged fruits described herein and 12 specimens of the associated foliage. They were collected from three sites of the Paleocene Fort Union Formation exposed in the Rock Springs Uplift in southwestern Wyoming. The holotype, collected by William P. Severn in 1954, was described by Brown (1956) who indicated that the site was in the upper lignite-bearing strata of the Fort Union Formation on the east side of the Rock Springs Uplift at US Geological Survey site 9344, NW 1/4 SW 1/4 sec. 36, T. 21 N., R. 100 W., ~7 miles (11 km) northeast of Point of Rocks, Wyoming (ca N41.7483012°, W108.6827727°, WGS84). This area has been mined extensively for coal (Jim Bridger Strip mine) since that time. Although we were unable to examine leaf fossils from the type locality, we studied new collections of leaves and fruits from two additional sites bearing more specimens of "*Koelreuteria*" *annosa* fruits, Big Flat Draw and Antelope Butte.

Fossil leaves and reproductive structures from the Big Flat Draw site, UF locality 15778, located at N41.3409500°, W108.8612167° (datum WGS84), were collected by Steven Manchester and students in 1985 and 1993. It is about 46 km south of the original site, also on the east flank of the Rock Springs Uplift. The shales at this site also yielded leaves of *Beringiaphyllum*, fruits of *Amersinia* (examples figured in Manchester et al., 1999), *Porosia* (Manchester and Kodrul, 2014), leaves of *Cornus swingii* (cited in Manchester et al., 2009) and *Aesculus hickeyi*, flowers of *Pistillipollianthus*, and some fern leaves.

The Antelope Butte site, UF locality 18016, is located on a south-facing canyon slope 1.7 km north of the indicated butte at N41.3978500°, W109.2059333° (datum WGS84) on the west flank of the Rock Springs Uplift. Specimens were collected from the upper portion of the exposed stratigraphy by Steven Manchester and students in 1988. At the same site, betulaceous leaves of *Corylites* and fruits of *Palaeocarpinus* are common (Correa-Narvaez and Manchester, 2022), along with occasional leaves of *Archeampelos acerifolia* (Newberry) McIver et Basinger. The winged fruits described here were not seen in our explorations of strata lower in the same canyon.

Specimens were initially observed with a Wild M5 dissecting microscope to investigate features of morphology and venation in detail. Some specimens were micro-excavated with dental tools and needles while observing under the dissection microscope to remove covering sediment and expose pedicel and/or style protrusions. Macrophotography was carried out with a Canon Rebel XSi camera with a 60-mm macro lens, using side-illuminated incandescent light, with digital images captured with the Canon EOS utility program. In many instances, differential pigmentation and staining of the fossils obscured venation patterns in macrophotography when standard reflected illumination was used (e.g. Fig. 1D–G). This problem was alleviated by using the Optical Shadow Effect mode of the Keyence VHX-7000N digital microscope to emphasize topographic relief, including features of the seeds, venation, perianth and style (e.g. Fig. 1C, H). Where indicated in figure captions, images of counterparts' halves of the same fruit were superimposed using Adobe Photoshop, with one of the images flipped horizontally in Photoshop to more fully reconstruct the original fruit.

Specimens with intact seeds were also investigated using a micro-CT scan with a GE Phoenix V|Tome|X M dual-tube nano-CT system at the University of Florida Nanoscale Research Facility. We used settings of 200 kV and 130 µA, capturing 2200 images at 200 ms, yielding a voxel size resolution of 25 µm. CT-generated volumes were processed with Amira vers. 6 to produce surface ply files that were imaged with MeshLab (Cignoni et al., 2008).

The length and width of leaves were measured with a cm ruler. Fruit dimensions, including length, width, pedicel length and width, locular width, and distance between lateral veins, were measured using the Fiji Image-J program. The averages of each parameter at each locality, and collectively, were calculated to identify relationships between localities and size. Plates were assembled using Adobe Photoshop to show variability in the specimens from Big Flat Draw, Antelope Butte and the notable features of these specimens, including seeds, venation, perianth and styles. In describing the fossils, we follow the terminology for fin-winged fruits used in Manchester and O'Leary (2010), and for features of venation of fruits and associated foliage, we consulted Ellis et al. (2009).

SYSTEMATICS

Genus **Pteleoidea**

Lopez del Rincon et Manchester **gen. nov.**

Etymology. The suffix -oidea meaning "resembling" is applied to *Ptelea* L. 1753 of the Rutaceae, dropping the letter a, for ease of pronunciation.

Generic diagnosis. Fruit winged, with an obovate outline, 1.1 to 2 times longer than wide, usually symmetrical; length 1.5–3.1 cm, width 1.0–2.1 cm. Apical portion rounded, with an abrupt apical emargination from which the style arises. Lateral margins smoothly convex over the upper 2/3, shifting to gently concave in the lower 1/3 and decurrent toward the base, with a swollen hypogynous disk and underlying whorl of five perianth remnants at the junction with the pedicel. Pedicel narrow, elongate, always retained by the dispersed fruit. Fruit composed of a pair of lateral wings adjoining a central, fusiform, locular area that averages about 65 percent of the fruit length and accommodates one or perhaps two small, ovate to elliptic seeds in axile placentation. Five to seven veins diverging from the fruit base and extending over the locular area. Lateral veins radiating from the locular area into both wings, moderately spaced, occasionally anatomising and dichotomizing, and extending distally to join a prominent marginal vein. Finer venation between the lateral veins forming a weak, irregular reticulum.

Type species. *Pteleoidea annosa* (R.W. Brown) Lopez del Rincon et Manchester comb. nov.

Pteleoidea annosa (R.W. Brown) Lopez del Rincon et Manchester **comb. nov.**

Figs 1–3

Synonymy.

1956 *Koelreuteria annosa* R.W. Brown.; J. Washington Acad. Sci. 46, p. 107, fig. 3; 1962, U.S. Geol. Surv. Prof. Pap. 375, p. 76, pl. 59, fig. 9.

Species diagnosis. Same as for genus.

Holotype. USNM42385 designated by Brown 1956. From USGS locality 9344, ~11 km north of Point of Rocks, Wyoming.

Epitypes. Additional specimens helpful in understanding the fruit morphology, which we designate as epitypes, include: UF15778-14138, 14144, 14141, 62742.

Additional specimens studied. From Big Flat Draw, Wyoming: UF15778-14135, 14136, 14137, 14142, 14145, 14146, 14147, 14152, 14154, 14155, 14158, 14160, 14162, 14172, 14173, 14080, 41902, 41903, 41908, 41923, 41924. From Antelope Butte, Wyoming: UF18016-22019, 22020, 13615, 13617.

Description. Fruit winged, with an obovate outline, usually symmetrical, length 1.5–3.1 cm, avg. 2.3 cm, width 1.0–2.1 cm, avg. 1.6 cm (n = 51), varying from 1.1 to 2.0 (avg. 1.4) times longer than wide. Apical portion generally rounded, but typically with a small emargination where the style protrudes (Figs 1B, E, I, J, 2E, 4A). Base grossly cuneate, lateral margins convex-rounded in apical 2/3, flexing to gently concave in lower 1/2, decurrent to the pedicel (Fig. 1A–J). Pedicel always retained by the dispersed fruit, narrow, ~0.4 mm wide, and up to 10.4 mm long (commonly reaching ~1/3 the length of the fruit; Fig. 1A–J). Fruit base subtended by a swollen hypogynous disk (Fig. 1C, F, G) and subtending perianth remnants with triangular calyx lobes (Fig. 2F). Fruit consists of a fusiform central locular area and a pair of lateral wings. The locule, measured from the point where central veins radiate to the point where they fuse back into the midvein, is 10.7–18.7 (average 15.3) mm long and 3.4–6.7 (average 4.9) mm wide. On average, the length of the locule was 65% of the total length of the fruit. A single stout style typically protrudes at the apex (Fig. 2E), yet some specimens show a cleft and possibly two stigmatic areas (Fig. 2D, C). Five to seven veins diverge from the fruit base and pass over the locular area (Figs 1C, J, 2G, I). Lateral veins, moderately spaced (0.48–1.25 mm, average 0.8 mm), radiating from the locular area into both wings, and extending to join a prominent marginal vein (Figs 1A, F, K, 2A, C, 4B). Lateral veins occasionally anastomose and dichotomise in course towards the margin. Venation between the lateral veins forms a finer, weak reticulum that is irregular in course (Figs 2C, G, 4B). Fruits accommodate one, perhaps two seeds which are ovate to elliptic, 3–6 (average 4) mm long, and 1–3 (average 2) mm wide (Figs 1G, H, 2B, H, I).

DISCUSSION

The populations of specimens that we studied from Big Flat Draw and Antelope Butte differ in their size ranges, with the former being larger (length 1.7 to 3.1 cm, average 2.4 cm, width 1.2 to 2.1 cm, average 1.7 cm) than the latter (length 1.5 to 1.6 cm, average 1.5 cm, width 1.0 to 1.5 cm, average 1.2 cm), so that the Antelope Butte specimens average only ~62 percent of the length of the Big Flat Draw specimens. However, the morphology seems to be identical, so we consider them to represent the same species. At both sites, the fruits appear to be mature, therefore the size discrepancy might reflect different environmental conditions.

Most specimens do not preserve obvious seeds, but shallow impressions of seeds were observed in three specimens (Figs 1G, H, 2B, H, I) revealing their shape and position. The seeds are elongate, elliptical to ovoid, and are situated on either side of the midline of the locular area, which indicates that it is possible for the fruit to contain two seeds, one in each of two adjoining locules, probably in axile placentation. It is

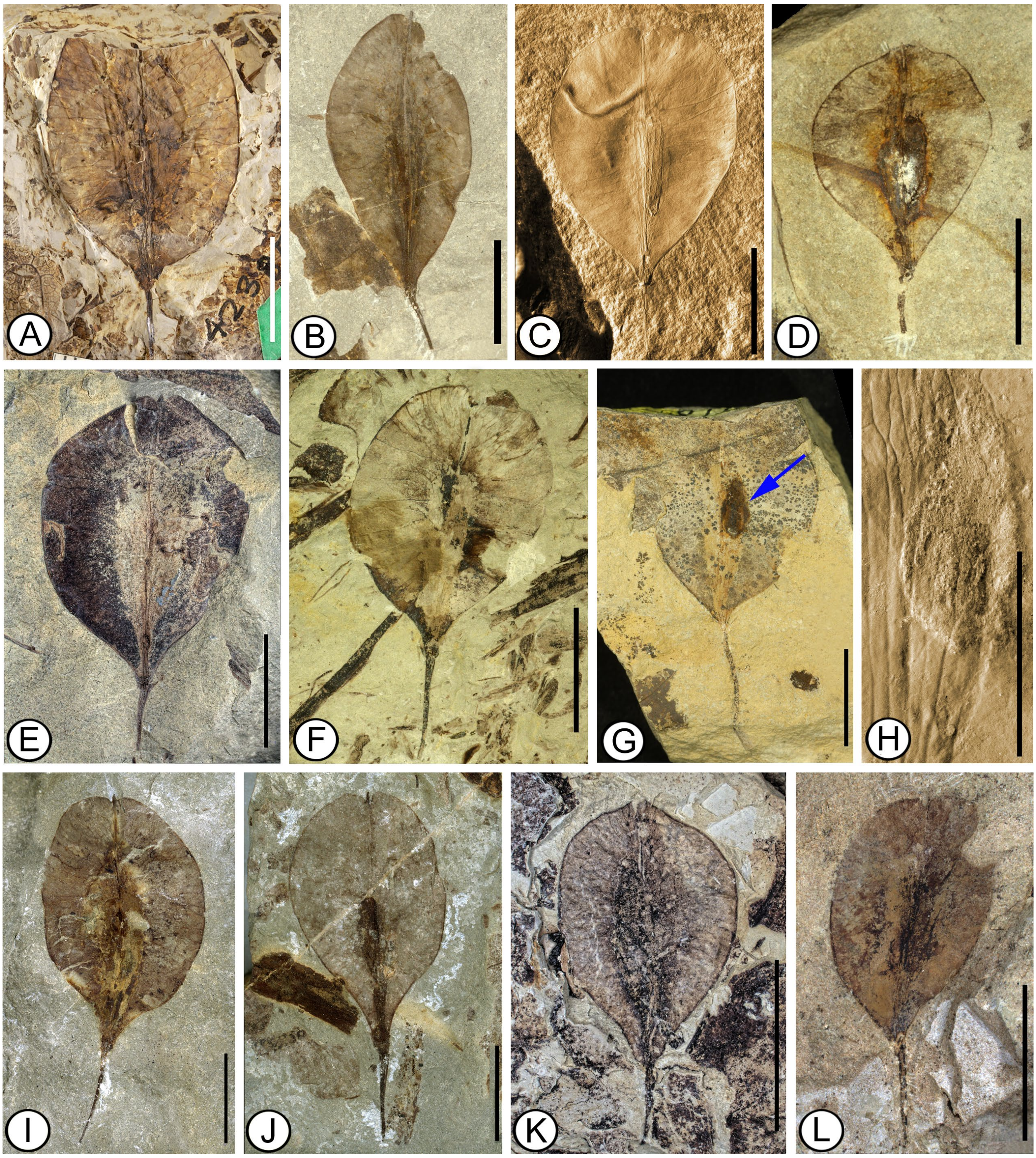

Figure 1. Fruits of *Pteleoidea annosa* (R.W. Brown) Lopez del Rincon et Manchester comb. nov. **A**. Holotype, USNM42385; from 7 mi NE of Point of Rocks, Wyoming; **B–J**. Specimens from Big Flat Draw, Wyoming; **B**. Narrow fruit with intact pedicel and stylar protrusion, UF15778-14138; **C**. Typical obovate fruit; Keyence shadow effect mode reveals central midvein extending from base to apex and six veins radiating from base and continuing over the locular area. Note lateral veins joining into a marginal vein, UF15778-14135; **D**. Obovate fruit with prominent marginal vein and fusiform central locular area, UF15778-14144; **E**. Fruit showing emarginate apex with protruding style. Composite image prepared from both counterpart specimens, UF15778-14080; **F**. Typical fruit showing how the lateral veins intersect abruptly with the marginal vein, UF15778-14147; **G**. Pedicellate fruit by reflected light, partly obscured by splotchy manganese stains. Arrow indicates position of the seed enlarged in H, UF15778-14162; **H**. Detail of seed impression, by Keyence shadow effect illumination, UF15778-14162; **I**. Fruit with accuminate base, intact pedicel and style, UF15778-14141; **J**. Fruit showing emarginate apex with protruding style, UF15778-62742A; **K**, **L**. Specimens from Antelope Butte, Wyoming; **K**. Fruit with well-preserved venation, UF18016-13617; **L**. Slightly asymmetrical fruit, UF18016-22020. Scale bars = 10 mm in A–G, I–L; 5 mm in H

noteworthy that these were the only seeds preserved in the 51 fruits examined. The seeds are weakly preserved, so convincing documentation was possible only with Keyence shadow-effect microscopy (Figs 1H, 2B) or micro-CT scanning (Fig. 2H, I). This may indicate that the seeds were more easily degraded than the surrounding fruit, or that many of the fruits lacked

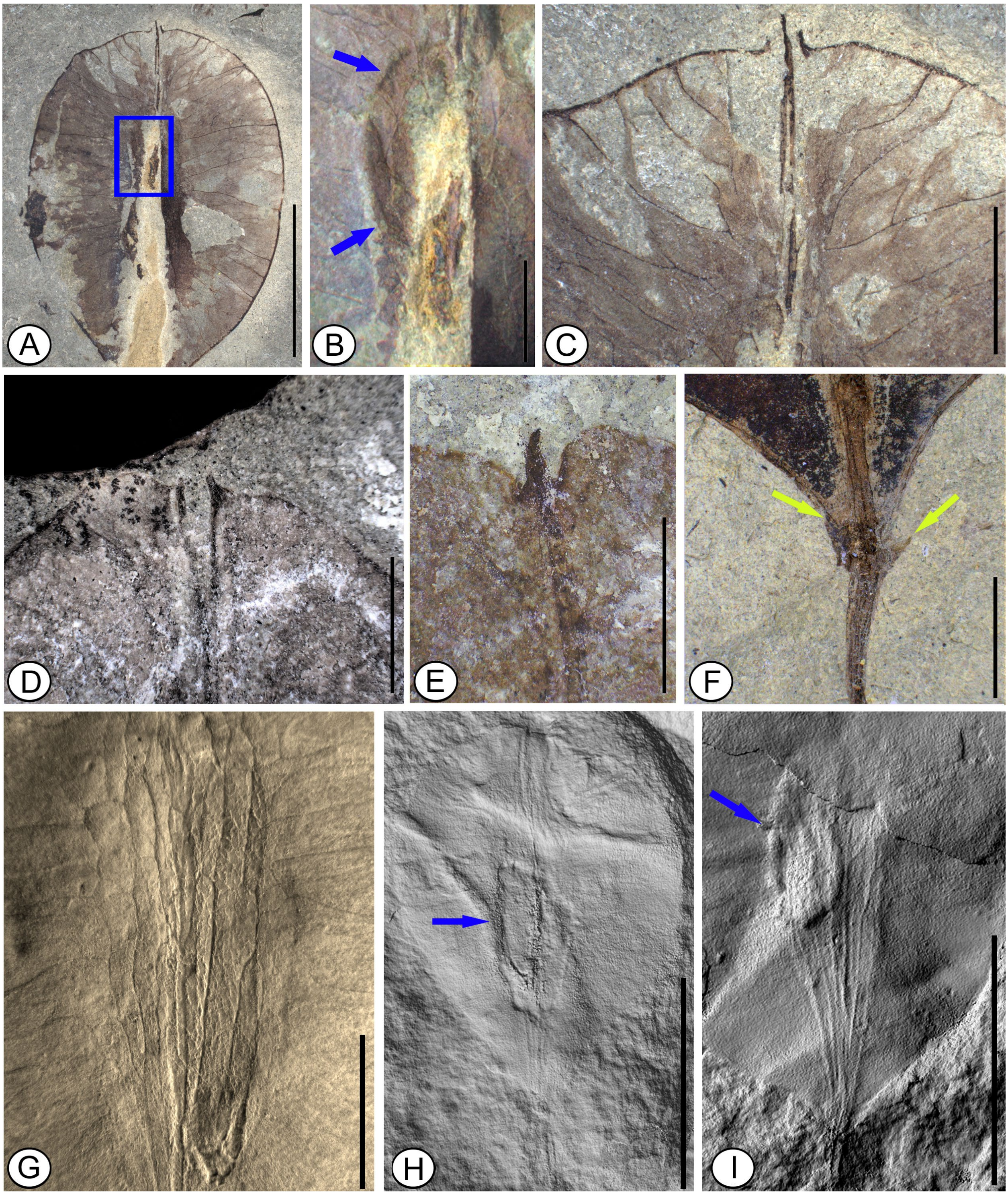

Figure 2. Fruits of *Pteleoidea annosa* (R.W. Brown) Lopez del Rincon et Manchester comb. nov. from Big Flat Draw, Wyoming. **A**–**C**. UF15778-41923; **A**. Fruit showing elliptical outline and well-preserved venation, including lateral veins that extend from the locular area to join the marginal vein. Blue rectangle outlining the area enlarged in B; **B**. Note blue arrows indicating curved outline of seed impression; **C**. Enlargement of apex showing separation of the marginal vein adjacent to the style, with another split occurring internally at the midvein towards the style. Note veins bifurcating one or two times towards the margin; **D**. Enlargement of apical portion of a fruit with an unusual case of apical cleft splitting the style into two arms, UF15778-62742B; **E**. Enlargement of specimen in Fig. 1J showing typical persistent style; **F**. Enlargement of specimen in Fig. 1E with yellow arrows indicating presence of two sharply-pointed sepals at the junction of the pedicel and base of the fruit. Note the prominent horizontal bulge of nectary disk at fruit base, UF15778-14080; **G**. Enlargement of specimen from Fig. 1C showing veins radiating from the base of the locule with reticulation, Keyence shadow effect, UF15778-14135; **H**. Micro-CT scan surface rendering of specimen from Fig. 1D showing veins radiating from the base of the locule and impression of seed (arrow), UF15778-14144; **I**. Micro-CT scan surface rendering of the specimen in Fig. 1G, H, showing basal divergence of veins, and ovate outline of the seed (arrow), UF15778-14162'. Scale bars = 10 mm in A–C, E–J; 2 mm in D

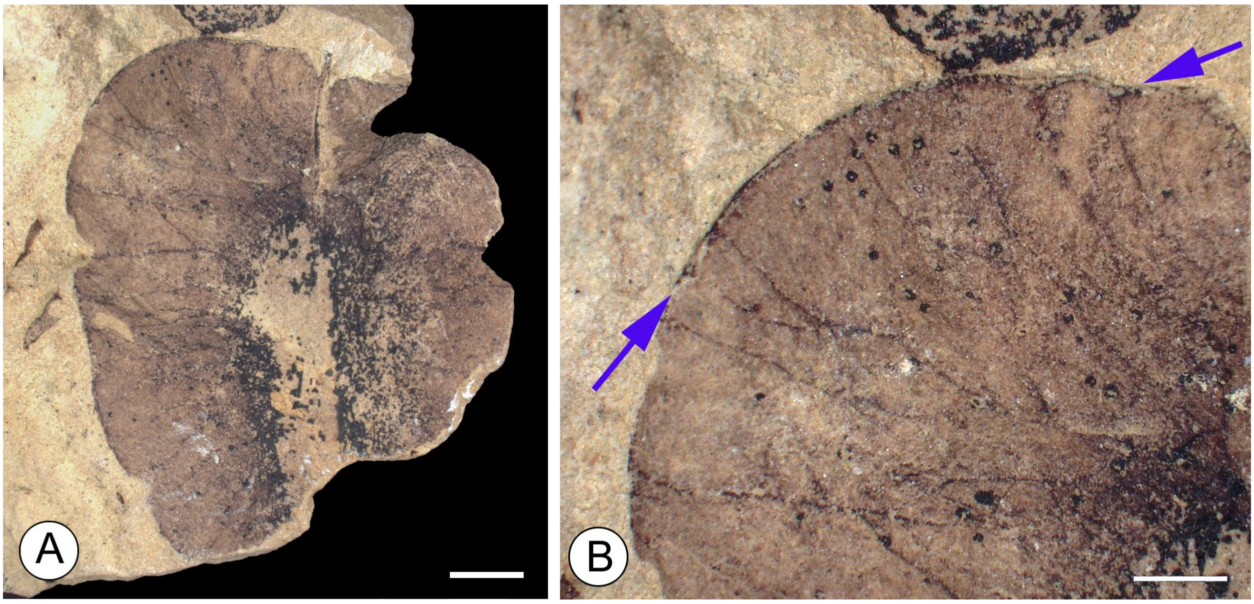

Figure 3. *Pteleoidea annosa* from Antelope Butte, Wyoming. UF18016-22019; **A**. Fragmented fruit with typical venation and protruding style; **B**. Enlargement showing lateral veins joining into a thick marginal vein (arrows). Note occasional cross veins, irregular reticulum of higher order veins. Scattered, orbicular dots are comparable to the dots found in associated leaflets. Scale bars = 2 mm in A, 1 mm in B

fertilized ovules. Or perhaps the fruits were dehiscent and seeds had been released at maturity. The fruits appear to lack any hint of a natural dehiscence area, but in three specimens, an apical slit bisecting the style and upper part of the fruit (Fig. 2C, D) might be an indication of a dehiscence opening. We suspect, however, that those splits are indications of damage and that the fruits were indehiscent.

The junction between the pedicel and the base of the fruit is swollen (Fig. 1A, C, F), indicating the former position of the perianth and nectar disk (see Fig. 2F). These features are consistent with Sapindales. One specimen retains intact sepals with triangular tips arranged in a whorl beneath the nectar disk (Fig. 1E, enlarged in Fig. 2F). The spacing of those sepals suggests that five were originally present. We infer from the two equally developed wings that these fruits probably developed from a bicarpellate ovary.

SYSTEMATIC POSITION

Brown (1956, 1962) considered this species, based on the holotype (refigured here, Fig. 1A), to represent a capsular valve of *Koelreuteria* (Sapindaceae). Extant fruits of that genus are bladder-like tricarpellate capsules that fall away from the pedicel into three separate valves (Fig. 4A–C). However, Brown's holotype and many of the subsequently collected specimens show only one pair of wings arising in a single plane with the pedicel still attached (Fig. 1A). *Koelreuteria* sheds its three valves separately, leaving the pedicel behind, so that it is only rarely preserved in contrast with *Pteleoidea*. Seeds of *Koelreuteria* are globose rather than ellipsoidal, and the locular area of *Koelreuteria* extends fully to the margin of each valve (Fig. 4C), so the valves lack the differentiated central fusiform locular area seen in *Pteleoidea*. Thus, the identification of these Paleocene fruits as *Koelreuteria* can be rejected. Convincingly identified fossil occurrences of *Koelreuteria* fruits are known from the Eocene onwards (Wang et al., 2013).

Pteleoidea fruits conform to the "fin-winged" fruit type that has evolved convergently in at least 45 different angiosperm families (Manchester and O'Leary, 2010). The number of wings present in fin-winged fruits ranges from 2 to 5 or more (up to 10) as summarized in Table 1 of Manchester and O'Leary (2010). Fruits with just two wings are found in one or more genera of the following families: Brassicaceae (*Brossardia* Boiss. 1841, *Fortuynia* Shuttlew. ex. Boiss. 1841, *Psychine* Desf. 1798, *Sameraria* Desv. 1815), Nyctaginaceae (*Abronia* Juss. 1789), Polygalaceae (*Monnina* Ruiz et Pav. 1798, *Phlebotaenia* Griseb. 1860, *Polygala* L. 1753), Sapindaceae (*Urvillea* Kunth 1821), Rutaceae (*Ptelea*, *Bottegoa* Chiov. 1916, *Spathelia* L. 1762), Cardiodipteraceae (*Cardiodipteris* Wall. ex Royle 1847), Hernandiaceae

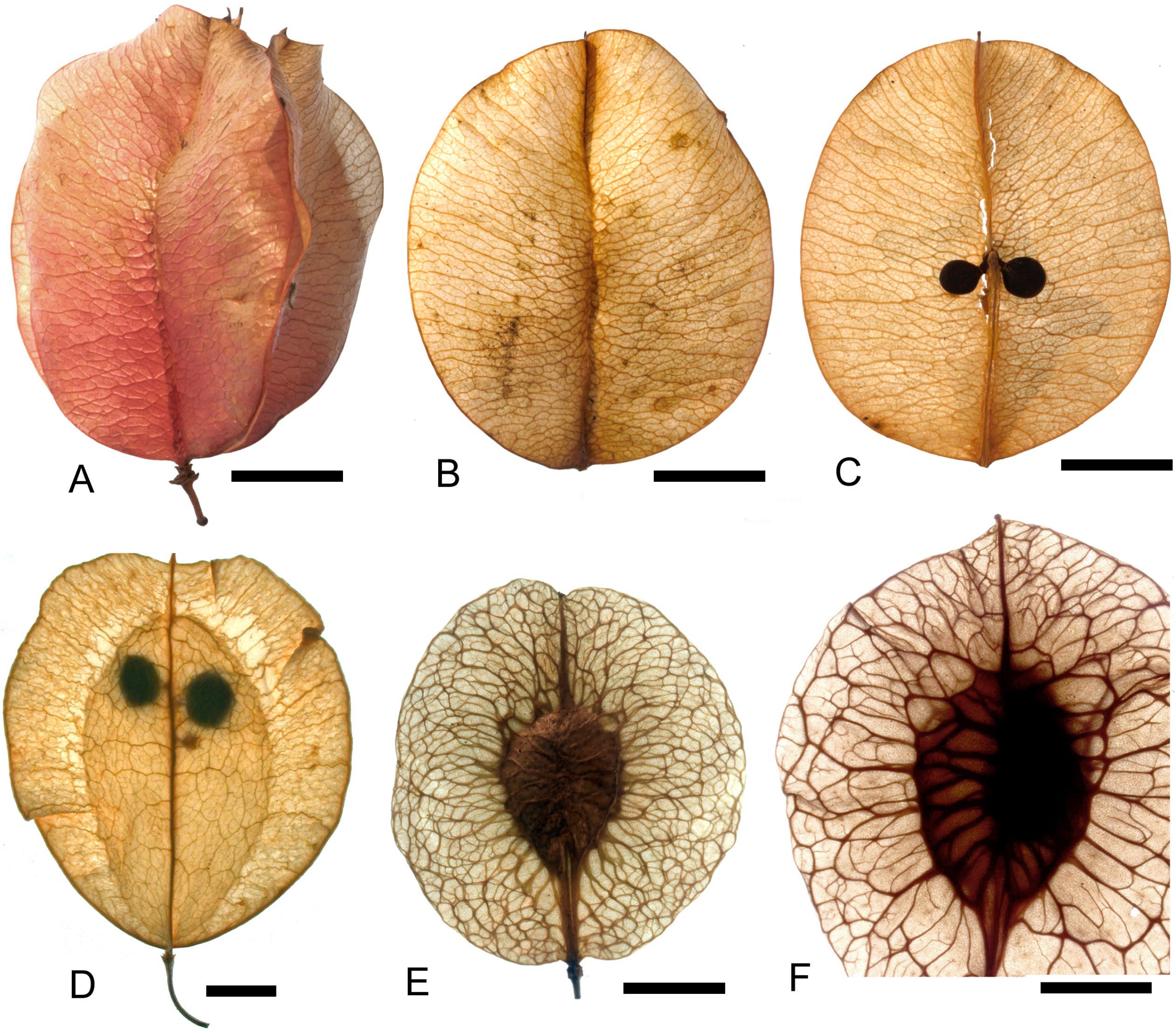

Figure 4. Extant fruits for comparison with *Pteleoidea*, illuminated with combined reflected and transmitted light; **A**–**C**. Sapindaceae: *Koelreuteria elegans* (Seem.) A.C.Sm. (UF mod. ref. coll. 2799, S. Manchester s.n. cultivated, Gainesville, Florida, USA); **A**. Complete bladder-like fruit with three valves, and intact pedicel; **B**, **C**. Isolated valves shed from the fruit and therefore lacking pedicels; **B**. Dorsal view of a valve showing lateral veins radiating from the median crease; **C**. Ventral view with pair of immature seeds; **D**. Brassicaceae: *Brossardia papyracea* Borss. (BARC: W.C. Haussknecht sn 1867, Near East). Biwinged fruit showing two orbicular seeds within an inflated locule that extends from the base of the fruit to more than three quarters to the distance of the apex. Note hypogynous perianth scar, thin pedicel, single protruding style, reticulate venation over locule and wings with some locular veins continuing into the wings, and strong marginal vein; **E**, **F**. Rutaceae: *Ptelea trifoliata* L. (FLAS: Easterday 856 Paynes Prairie, Florida, USA); **E**. Bi-winged fruit showing thin pedicel, thick scar of perianth and nectary, central locular area occupying middle third of the main axis, with a few veins rising from base that radiate up to the bottom of the locular area; Reticulate veins braid over the locular area, continuing out into the wing. A strong midvein continues from the top of the locular area to the base of the style. Note the discontinuous marginal vein formed partly by the looping of distal veins of the reticulum; **F**. *P. trifoliata* (UF mod. ref. coll. 1742, V. Call sn, Bloomington, Indiana, USA). Note three veins extending from the base; one midvein and two lateral veins that enter into the reticulum covering the locular area. Contains a single ovate seed (dark silhouette) that is visible on the right hand side of the locular area. Scale bars = 10 mm in A–C, 5 mm in D–F

(*Iligera* Blume 1827), Combretaceae (*Pteleopsis* Engl. 1894), Cucurbitaceae (*Pteropepon* Cogn. 1916, *Pseudosicydium* Harms 1927, *Sechiopsis* Naudin 1866) and Asteraceae (*Anacyclus* L. 1754, *Boltonia* L'Hér. 1788, *Verbesina* L. 1753, etc.). As *Pteleoidea* is characterized by a superior ovary, we can eliminate taxa with inferior ovaries, such as Combretaceae, Cucurbitaceae and Asteraceae. Fruits of the other families listed are readily distinguished by differences in venation and locule configuration as documented in Manchester and O'Leary (2010). Although similar fruits occur in the brassicaceous genus *Brossardia* (Fig. 4D), the perianth in Brassicaceae is generally 4-parted rather than 5. Features of wing venation, including vein density, vein course, and presence or absence of a marginal vein in each of the genera mentioned above, help to distinguish each of them from *Pteleoidea*.

Features observed in *Pteleoidea* that are important for assessing its affinity among extant angiosperm clades include a superior, syncarpous, two-carpellate ovary with axile placentation, a few seeds (one or perhaps two per carpel), a narrow pedicel, and a nectary disk present at the base of the gynoecium. These features are consistent with placement in Sapindales (Stevens, 2001 onwards).

Among the modern genera surveyed, extant *Ptelea* (Rutaceae), a genus with indehiscent winged fruits, appears most similar to *Pteleoidea* in shape of the wings, the narrow pedicel, presence of a superior ovary, persistent apical style, and elongate-elliptical shape of the seeds. However, there are noteworthy differences. The marginal vein of *Ptelea* (Fig. 4E, F) is weak and incomplete in comparison to *Pteleoidea*, which has a thick and continuous marginal vein (Figs 2C, 3B). Both extant and fossil species of *Ptelea* (Call and Dilcher, 1995) have a different venation pattern, with reticulum having areoles that are not as elongate as those in our fossil. In *Ptelea*, the reticulate venation over the locule is much more prominent (compare Fig. 4F with Figs 1H, 2G). Furthermore, in *Ptelea*, the region between the base of the fruit and the base of the locule has only three veins diverging in the axis of symmetry, whereas *Pteleoidea* has multiple veins fanning out over the locule (Fig. 2I). This continuous divergence of the veins from this region is not observed in *Ptelea*. Although *Ptelea* is known by fossil fruits from other sites, including the Miocene of Oregon (Call and Dilcher, 1995) and the Eocene of Utah (Manchester and O'Leary, 2010), the morphological differences from *Pteleoidea* support recognition of the latter as a distinct genus.

ASSOCIATED FOLIAGE

Both of the sites where we conducted original fieldwork, Big Flat Draw and Antelope Butte, Wyoming, preserve numerous fossil leaves, but the diversity is relatively low (main taxa listed in the material and methods above). By a process of elimination, we are able to infer the most likely leaf candidate to have been produced by the *Pteleoidea* plant. The apparent lack of such leaflets at other Paleocene sites across the Rocky Mountain and Great Plains region (Brown, 1962; Manchester, 2014) provides another hint that these might represent the foliage of *Pteleoidea*, because the distinctive fruits also have not been recovered from those other sites.

The best candidate foliage for *Pteleoidea* seems to be a finely serrate leaflet with numerous closely spaced circular glandular dots scattered over the entire surface (Fig. 5). Although we hypothesize that these leaflets may originate from the same plant as *Pteleoidea* fruits, proof of a physical connection remains absent. The specimens we examined are UF15778-14094, 14096, 14098, 14104, 14105, 14109, 14110, 14139 from Big Flat Draw and UF18016-13597, 22035, 22036, 22038 from Antelope Butte.

The laminae are interpreted as leaflets rather than simple leaves because of their strong basal asymmetry and short petiolules (Fig. 5A, D). The leaflets are typically elliptical, 8.5–12 cm long, 3 to 4 cm wide, and are 2.2 to 4 times longer than wide. The secondary veins are pinnately organized, weak and somewhat wavering in course, and are camptodromous, looping well inside the margin. Intersecondary veins are up to one per intercostal area and parallel to adjacent secondary veins. Tertiary veins are weak and form an irregular reticulum (Fig. 5B, E). The laminae possess inconspicuous glandular teeth regularly spaced on the margin (Fig. 5C, F), and at higher magnification the leaf surface has numerous evenly scattered dark dots (Fig. 5G, H). These dots are similar in form and distribution to pellucid dots found in extant Rutaceae (Kubitzki et al., 2010).

Rutaceae and related families of the Sapindales frequently possess pinnately compound leaves. Although pellucid dots are a prominent feature of the leaflets, we have not verified their presence on most *Pteleoidea* fruits. One fruit specimen from Antelope Butte (UF18016-22019) displayed dots sporadically on the fruit's wings (Fig. 3) that are similar in size and distribution of those on the leaflets. However, the dots were concentrated into patches on the fruit rather than uniformly distributed throughout the fruit wings. Thus, the spots on this specimen might represent fungal bodies rather than pellucid dots.

As far as we are aware, *Pteleoidea* was endemic to North America and relatively limited in distribution geographically, despite the widespread distribution of the genera with which it co-occurred, including *Cornus*, *Amelanchier*, *Palaeocarpinus*, and *Porosia*. If our hypothesis of the relationship to Rutaceae is accepted, it adds to the evidence that this family was diversifying in the early Cenozoic. Another extinct genus of rutaceous fin-winged fruits, known as *Quinquala* Manchester et Disney, was distributed in the Eocene of Wyoming

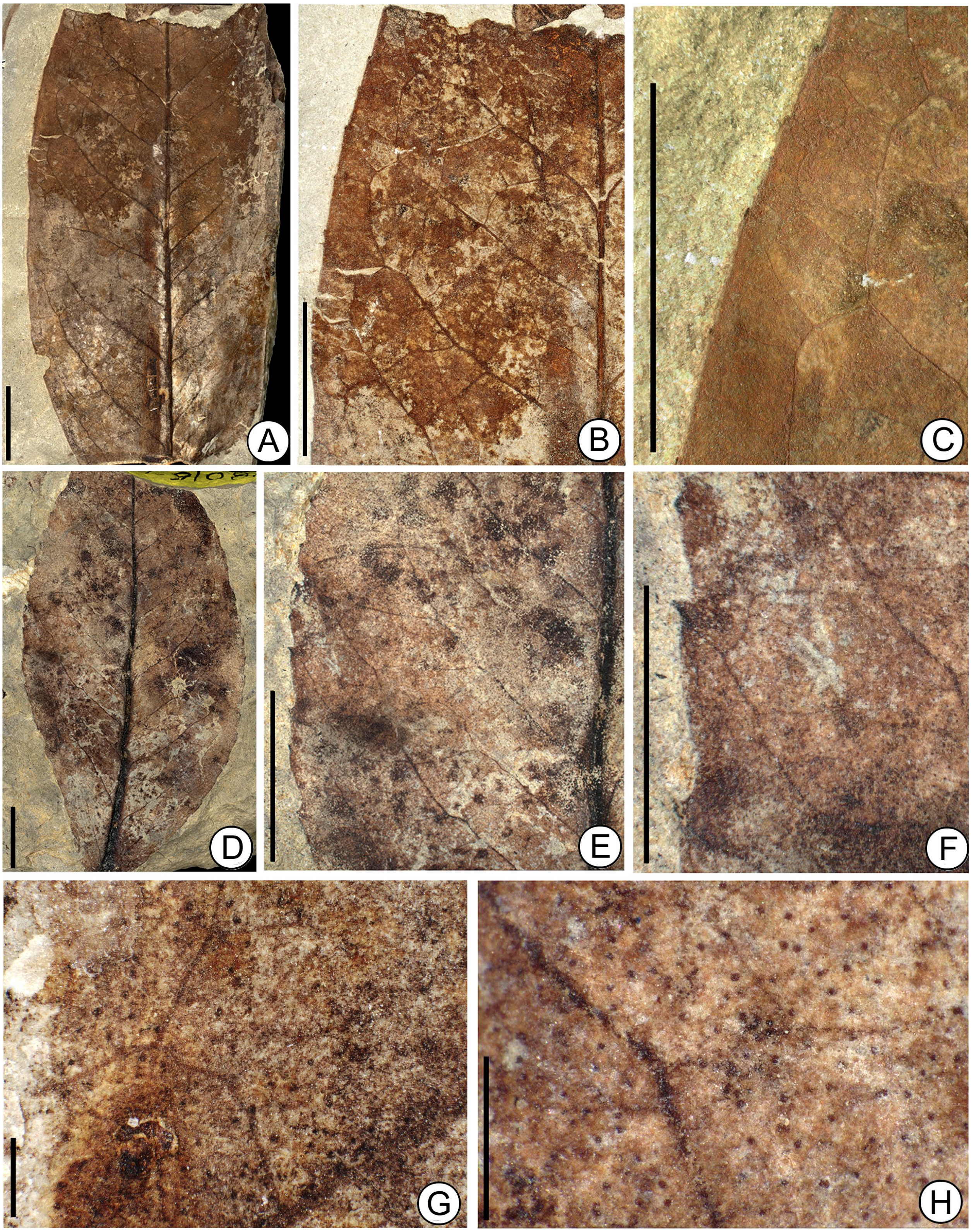

Figure 5. Foliage associated with *Pteleoidea* fruits; **A**–**C**. UF15778-14109 from Big Flat Draw, Wyoming; **A**. Leaflet showing thin, pinnate secondary veins; composite image from both counterparts; **B**. Enlargement showing thin, somewhat sinuous secondary veins looping well within the margin, and weak tertiary veins; **C**. Greater enlargement showing glandular teeth and associated venation; **D**–**F**. UF18016-13597 from Antelope Butte; **D**. leaflet showing thick midvein with thinly pinnate secondary veins; **E**. Enlargement of Fig. 4D showing secondary veins looping near toothed margin. Tertiary venation is irregular; **F**. Greater enlargement showing thick, deep, glandular teeth and secondary looping; **G**. Enlargement from Fig. 4D showing scattered dots over leaflet surface; **H**. Enlargement from Fig. 4D showing dots. Scale bars = 10 mm in A–E, 5 mm in F, 1 mm in G–H

and Oregon (Manchester et al., 2020), and the extant genus *Ptelea* can also be traced to the Eocene (Manchester and O'Leary, 2010). Along with fruits of *Porosia*, known from the Late Cretaceous and Paleocene of North America and Asia (Manchester and Kodrul, 2014), *Pteleoidea* is among the earliest known fossils of likely rutaceous affinity.

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