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The Paleocene Horse Creek florule, Tongue River Member of the Fort Union Formation, southeastern Montana, USA

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ABSTRACT. We investigated leaf, cone and fruit impressions preserved in a siltstone deposit between coal seams in the late Paleocene Tongue River Member near Otter, southeast Montana, to assess the floristic diversity and composition. We document the presence of *Taxodium* based on seed cone scales as well as foliage branches and associated pollen cones, and a low-diversity angiosperm assemblage of about 15 genera dominated by Platanaceae (*Platanus, Macginitiea, Macginistemon*) and Cornales (*Cornus, Davidia, Amersinia*, *Browniea*), cf. Trochodendraceae (*Zizyphoides*, *Nordenskioeldia*), augmented by *Aesculus*, *Trochodendroides*, *Ulmites* and *Porosia*. Most of these genera were widespread in the Paleocene of the Northern Hemisphere. The low diversity of this florule is consistent with that of Tiffanian assemblages elsewhere in Montana and Wyoming. The leaf known as *Phyllites demoresii* Brown is proposed as a likely candidate to correspond with the extinct fruits called *Porosia verrucosa* (Lesquereux) Hickey emend. Manchester et Kodrul.

KEYWORDS: coal, fossil leaves, Cornales, Platanaceae, *Aesculus, Ulmus, Porosia*

INTRODUCTION

The Paleocene flora of the Rocky Mountains and Great Plains region is known from more than 500 collection sites spreading from New Mexico to Alberta and has been treated collectively in many publications (summarized in Brown, 1962; Hickey, 1977; Peppe, 2010; Pigg and DeVore, 2010; Manchester, 2014). Relatively few individual sites have been treated in detail to provide glimpses of particular settings and times. Examples include Bison Basin of the Fort Union Formation in Wyoming (Gemmill and Johnson, 1997), Ravenscrag Butte of the Ravenscrag Formation in Saskatchewan (McIver and Basinger, 1993; West et al., 2021), the Almont flora in the Sentinel Butte Formation of North Dakota (Crane et al., 1990; Zetter et al., 2011), and the Castle Rock (Ellis et al., 2003), West Bijou (Barclay et al., 2003) and Littleton floras (Huegele and Manchester, 2020) in the Denver Formation of Colorado.

Here we focus on the floristic composition of a single collecting site in the Tongue River Member of the Fort Union Formation in southeastern Montana to give insight into the community of plants surrounding the site of deposition. The preservational quality is excellent for details of leaf outline and venation and the morphology of fruit and seed impressions in the siltstone. We refer to this as the Horse Creek florule, which may be considered a subset of the broader Fort Union flora known from numerous sites or florules in Montana and Wyoming. The purpose of this article is to identify the leaves and reproductive structures

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preserved in the Horse Creek florule and use them to infer the local environment of this region about 62 million years ago.

MATERIALS AND METHODS

The locality (Fig. 1) was discovered in 2002 adjacent to a burning underground coal seam, and was collected several times during one and two-day visits in summers 2003, 2007, 2013 and 2014, resulting in a collection of about 230 specimens deposited at the Florida Museum of Natural History at University of Florida, Gainesville (UF). It is 1.5 km west of USGS locality 8888 [between Elk and Wall coal beds, visited by R.W. Brown and R.P. Bryson in September 1940]. Siltstones and shales close to the heat of the burning coal became more durable and easier to cleave along the bedding planes. The productive siltstones and shales are about 1 m thick and exposed over an area of 3 × 8 m, on the west side of a road cut on a portion of Montana highway 484 (Otter Creek Road) that was abandoned when the main road was straightened

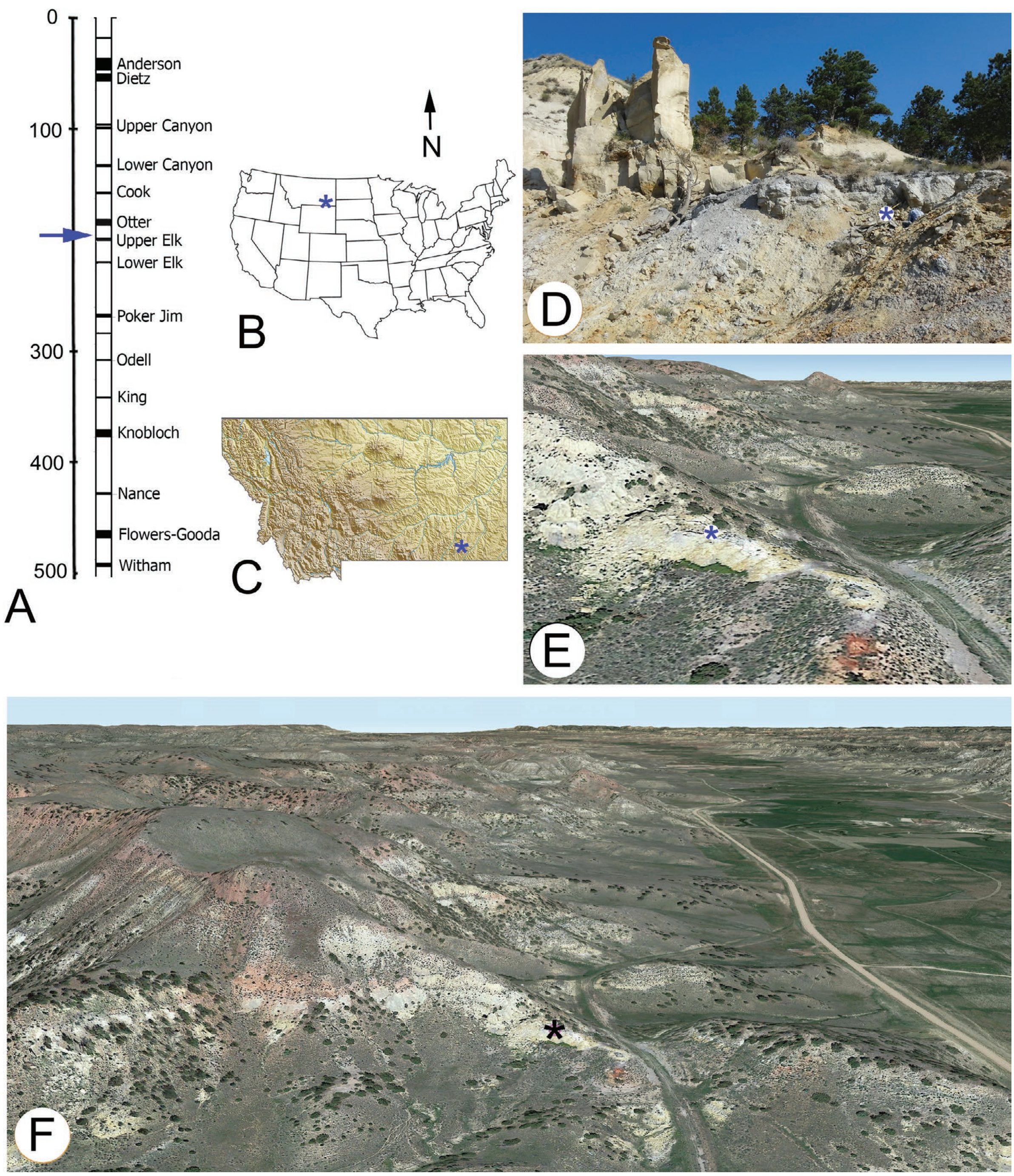

Figure 1. Horse Creek paleobotanical site. **A**. Stratigraphic position of the Horse Creek locality (arrow) in relation to locally mapped coals; scale in meters (Culbertson, 1987); **B**, **C**. Index maps of United States and Montana, with asterisk (*) indicating location of the Horse Creek locality; **D**. Site of quarrying (*), looking northeastward; **E**. Stratigraphy at the site, looking northward, Google Earth; **F**. Overview, looking northward, road 484 along right, Google Earth

(Fig. 1F). The site is located at 45.2643194°N, 106.1611389°W in Custer National Forest in Powder River County, southeastern Montana (Fig. 1B–F).

These strata were recognized as Tongue River Member of the Fort Union Formation by Bryson and Bass (1973) who mapped coal beds throughout the local area. The Tongue River Member is characterized by interbedded thick beds of light-yellow-gray sandstone, sandy shale, and gray, sometimes carbonaceous, shale, and includes in this region about thirty thick coal beds. The fossil site is positioned about 9 m below the Otter coal bed and immediately above the Upper Elk coal bed (Fig. 1A). Culbertson (1987) mapped the coals across this region using well core and outcrop data and showed that the Otter coal is well above the Knobloch coals and beneath a sequence of successively younger coals named Canyon, Dietz, Anderson and Smith (Fig. 1A). Hence these strata are older than the Anderson and Smith coal beds studied palynologically in the same basin in Wyoming by Pocknall and Flores (1987).

The Tongue River Member is 425 to 485 m thick in the Moorehead coal field, which includes this site (Bryson and Bass, 1973). The age of the Tongue River Member has been estimated based on paleomagnetic correlations to range from 62.8 to 61.5 Ma in sediments exposed at Signal Butte near Miles City ~115 km to the north (Peppe et al., 2011). The Newels Nook vertebrate fauna and associated fruit and seed collection from the level of the lowest coal of the Tongue River Member on the western edge of the Powder River Basin 85 km west-northwest of Horse Creek was judged to be lower Tiffanian, or about 60 Ma (Robinson and Honey, 1987; Huegele and Manchester, 2022).

Specimens were photographed with a Canon XSI camera or Nikon D-200 SLR digital camera and illuminated using a pair of incandescent lights adjusted to appropriate angles to highlight venation detail. In the case of a poorly pigmented but well impressed *Aesculus* leaf, superior results were obtained using low-angle sunlight just prior to sunset. Terminology for the description and discussion of leaf architecture follows Hickey (1973) and Ellis et al. (2009).

Some of the cone scale and fruit remains were investigated by micro-computed tomography (µCT). For this purpose, we used a GE Phoenix V|tome|xm240 CT scanner with a tungsten reflection target, at the University of Florida College of Engineering Nanoscale Research Facility. Voltage was set at 180 kV, and a current at 80 µA, and 2000 images, at 131 ms each, were taken at a voxel size of 31 µm. These scans were processed in VG Studio Max (ver. 3.1; Volume Graphics, Charlotte, NC), Avizo (version 9.0 Lite; FEI Visualization Science Group, Hillsboro, Oregon) and Meshlab (Cignoni et al., 2008).

RESULTS

SYSTEMATIC PALEOBOTANY

Most of the fossils have been identified with confidence to the genus level with exception of a few entire-margined leaves. We recognize 16 species, when adjusted for overlapping fruit/leaf names as summarized in Table 1. The taxa include one fern, a horsetail, one conifer, and about a dozen angiosperms.

Class POLYPODIOPSIDA Cronq., Takht. et W. Zimm.

Family EQUISETACEAE Michx. ex. DC.

Genus *Equisetum* L.

Equisetum sp.

Fig. 2A

Description. Stem ~2 cm wide with distinctive longitudinal ridges and one horizontal joint with a whorl of circular branch scars, each ~0.5 mm in diameter.

Specimen examined. UF 18969-60476A.

Discussion. As noted in Brown (1962), characters such as leaf sheath and number of leaves for Paleocene *Equisetum* vary greatly

Table 1. Taxonomic composition of the Horse Creek florule

Category	Vegetative	Reproductive
Equisetaceae	*Equisetum* sp.	
Ferns	cf. *Dennstaedtia americana*	
Cupressaceae	*Taxodium ulrichii*	*Taxodium ulrichii*
Platanaceae	*Platanus* sp.	
Platanaceae	*Macginitiea gracilis*	*Macginistemon mikanoides*
cf. Trochodendraceae	*Zizyphoides flabella*	*Nordenskioeldia borealis*
Cercidiphyllaceae	*Trochodendroides genetrix*	
Ulmaceae	*Ulmites microphylla*	
Sapindaceae	*Aesculus hickeyi*	*Aesculus hickeyi*
cf. Rutaceae		*Porosia verrucosa*
Nyssaceae	*Browniea serrata*	*Browniea serrata*
Nyssaceae	*Davidia antiqua*	*Davidia antiqua*
Indet.	*Phyllites demoresii*	

and are not readily distinguishable into species, thus we identify this specimen as *Equisetum* sp. The single stem collected from Horse Creek is relatively large (2 cm wide) compared to most extant *Equisetum* which typically are up to 1 cm wide, although extant giant horsetails from South America have tall stems that can be up to 4 cm wide (Husby, 2013).

Family Indeterminate

cf. *Dennstaedtia americana* Knowlton

Fig. 2B

Description. Sterile foliage, length 3 cm, width 1.7 cm; pinnules shallow-lobed or sometimes crenulate, with a weakly defined midvein that is similar in thickness to the secondary veins that depart from it. Secondary veins dichotomizing 1 to 3 times, craspedodromous.

Specimen examined. UF 18969-34532.

Discussion. A single specimen of sterile foliage was recovered which matches the form of the pinnae that Brown (1962) described as *Dennstaedtia americana* Knowlton from other sites of the Fort Union Formation. We have not seen fertile material from this site so the generic identification remains tentative. Even with fertile material, there are convergent morphological features in *Dennstaedtia* and members of the tree fern families Dicksoniaceae and Cyatheales that can make it difficult to confirm the identification to *Dennstaedtia* unless features of the annulus are well preserved, as has been shown for *D. christophelii* Pigg, Greenwood, Sundue et DeVore in the Eocene of western North America (Pigg et al., 2021).

Order PINALES Gorozh.

Family CUPRESSACEAE Gray

Genus ***Taxodium*** Rich.

Taxodium olrikii (Heer) R.W. Brown

Figs 2C–H, 3

Description. Needle leaves on twigs, seed cones scales, and pollen cones. Leaves alternate on twigs, linear with acute apices, 6.7 mm long and 1.0 mm wide. Twigs with prominent scars. Seed cone scales shed at maturity, obovate, average size of 14 mm × 11 mm, possessing a horizontal median umbo. Pollen cones in clusters, each cone in axil of scale like bract, cones obovate to circular, average 3.2 mm long and 2.8 mm wide.

Specimens examined. UF 18969-34525, 34533–34535, 34537, 34538, 34549, 34614, 50974.

Discussion. Although Brown (1962) recognized *Taxodium* to be present in the Fort Union Formation, Manchester (2014) questioned the identification because it was based only on leaves, without accompanying cone material, whereas *Glyptostrobus*, with similar foliage, is represented by cones, cone scales and seeds. At Horse Creek, we found the distinctive shed cone scales of *Taxodium*, along with pollen cones and foliage also consistent with *Taxodium*. The deciduous leafy twigs of *Taxodium* produce distinctive scars on the parent twigs, some of which are found at Horse Creek.

Other taxoidioid Cupressaceae known from the Fort Union Formation include *Metasequoia* and *Glyptostrobus*, but we did not find evidence for these genera in the Horse Creek assemblage. *Metasequoia* would be distinguished easily by the opposite organization of its leaves and pollen cones. *Glyptostrobus* would be more difficult to distinguish based on foliage alone, but it has smaller, more elongate cone scales that are apically serrate (Brown, 1962; Li et al., 2018).

We follow the nomenclature adopted by Brown (1962) who attributed his material to the species *T. olrikii* (Heer) R.W. Brown which is based on leafy twigs from the Paleocene of Atanikerdluk, Greenland (originally *Taxites olrikii* Heer 1868).

ANGIOSPERMS

Order TROCHODENDRALES
Takht. ex Cronq.

Family cf. TROCHODENDRACEAE Eichl.

Zizyphoides flabella
(Newberry) Crane, Manchester et Dilcher

Fig. 4A–D

Description. Leaves with long narrow petioles and narrow to widely elliptical, ovate, or obovate laminae that vary from entire-margined

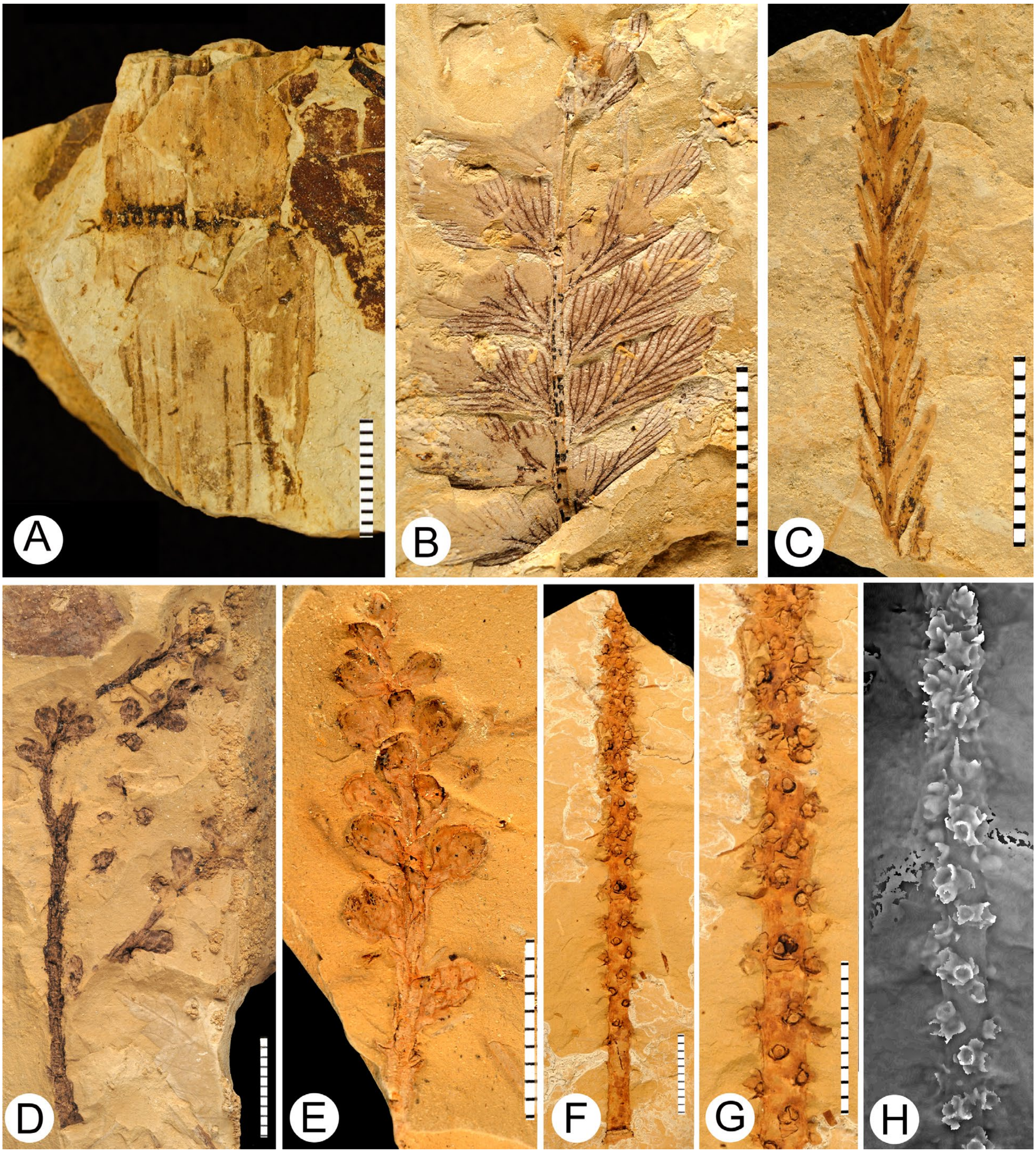

Figure 2. Horsetails, ferns, conifers. **A**. *Equisetum* sp. UF 18969-60476A; **B**. cf. *Dennstaedtia americana* Knowlton, UF 18969-34532; **C–H**. *Taxodium olrikii* (Heer) R.W. Brown; **C**. Leafy branchlet, UF 18969-34525; **D**, **E**. Pollen cones; **D**. Cones on leafy twig, UF 18969-50974; **E**. UF 18969-34549; **F–H**. Twig with distinctive scars; **F**. UF 18969-34614; **G**, **H**. Enlargement from F.; **H**. Micro-computed tomography of G. Scale bars = 10 mm in A–G; bar in G applies also to H

to crenate in the upper half of the lamina. Venation acrodromous with three or five major veins arising from the base, commonly with agrophic veins. Veins connecting between the major (primary and secondary) veins forming percurrent convex arches. Secondary and tertiary veins forming brochidodromous loops near the margin, or semicraspedodromous and bifurcating with one branch curving to join the supraadjacent secondary vein and the other extending directly to the marginal crenation tipped by a prominent gland. Higher order venation forming a fine reticulum with polygonal areoles.

Discussion. These leaves correspond to the widespread species of Late Cretaceous and Paleocene species *Zizyphoides flabella* (Crane et al., 1991; Zolina et al., 2021). The long slender petioles (Fig. 4A), palmate venation (Fig. 4A–C), and ovate to obvovate lamina with entire to

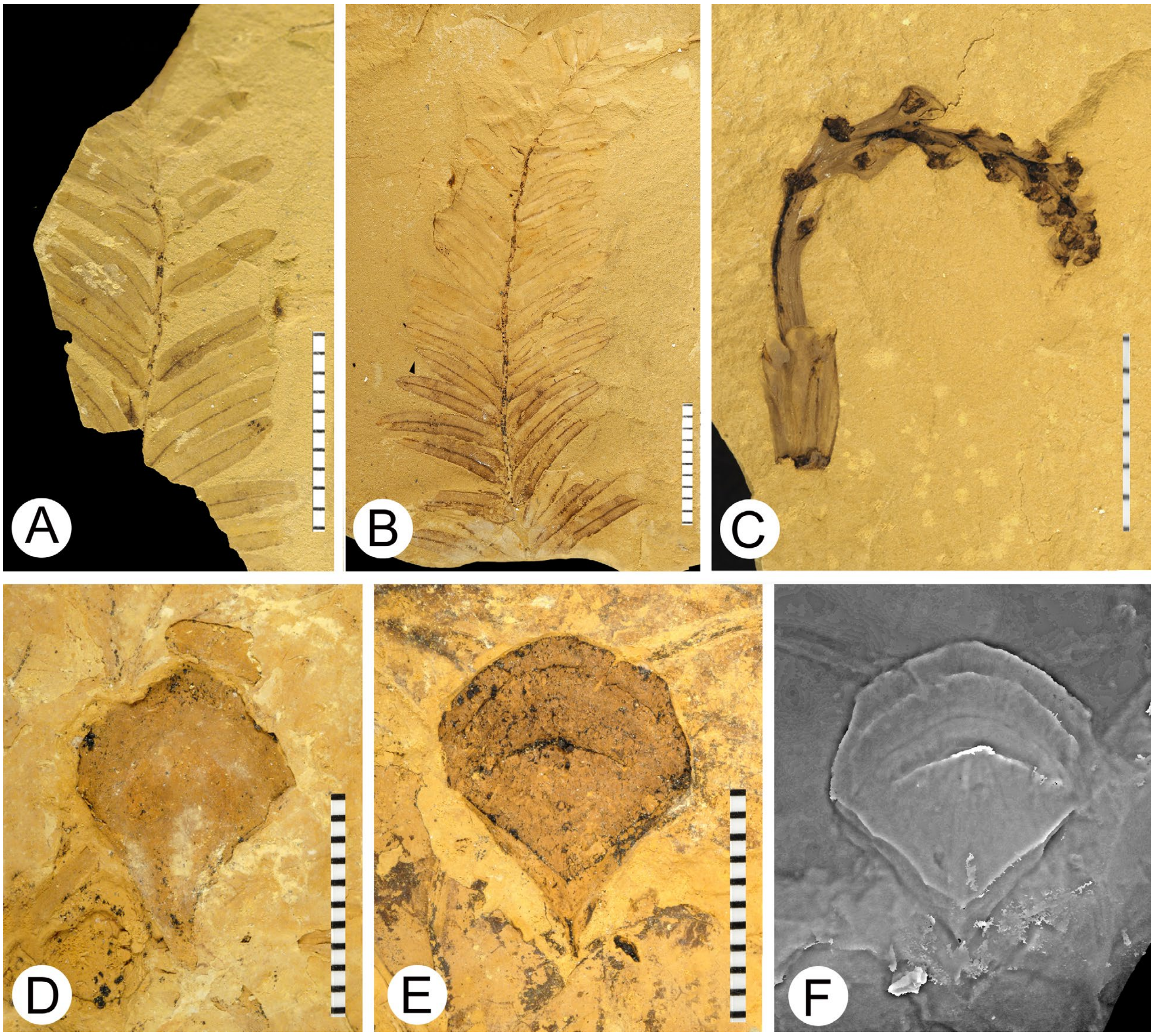

Figure 3. Cupressaceae. *Taxodium olrikii*. **A**, **B**. Leafy branchlets; **A**. UF 18969-34538; **B**. UF 18969-34538; **C**. UF 18969-34537; **D**–**F**. Cone scales; **D**. UF 18969-34534; **E**, **F**. UF 18969-34535; **E**. Reflected light; **F**. Micro-computed tomography. Scale bars = 10 mm in A, B, D, E (applies also to F); 5 mm in C

crenate margins are distinctive. The crenations have distinctive apical glands (Fig. 4D).

Specimens examined. UF 18969-50975, 60475, 61744.

Nordenskioeldia borealis Heer

Fig. 4E–K

This distinctive fruit type occurs in association with *Zizyphoides* leaves at numerous Paleocene sites throughout the Northern Hemisphere (Crane et al., 1991). In the Horse Creek collections, we observed an axis that had shed its fruits, with distinctive persistent sessile receptacles (Fig. 4E, J), a portion of intact fruit with four radiating fruitlets (Fig. 4F–H) and isolated D-shaped fruitlets (Fig. 4G–I). The identity of these isolated parts as belonging to the same taxon is confirmed by more complete specimens in various stages of shedding from other sites (Crane et al., 1991; Wang et al., 2009).

Specimens examined. UF 18969-34510, 34519a, b, 61727.

Order PROTEALES Juss. ex Bercht. et J. Presl

Family PLATANACEAE T. Lestib.

Genus ***Platanus*** L.

Platanus **sp.**

Fig. 5A–E

Description. Leaves ovate to faintly trilobed. Base of lamina obtuse to rounded, lobe apices

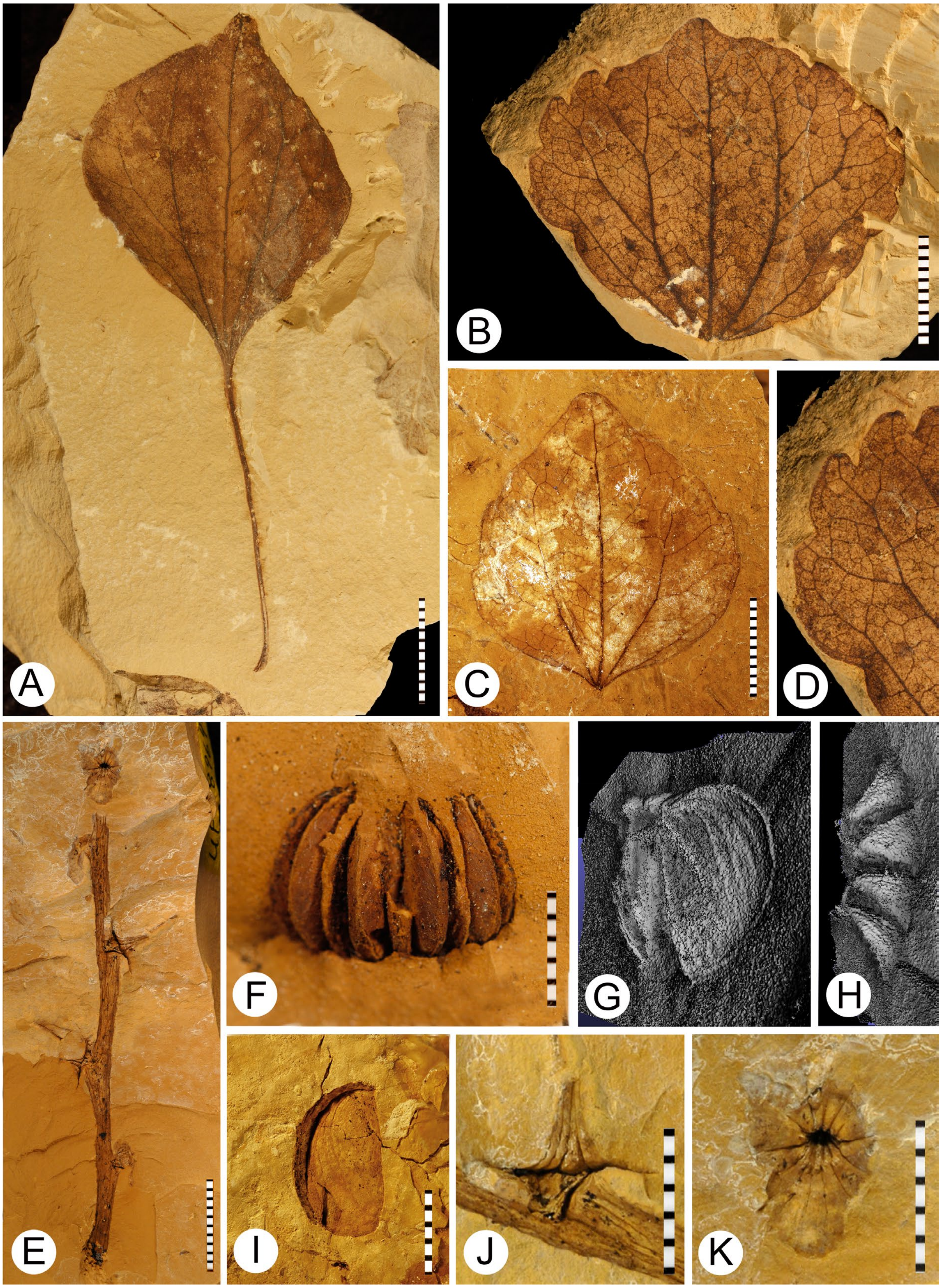

Figure 4. cf. Trochodendraceae. **A**–**D**. *Zizyphoides flabella* leaves. **A**. Leaf showing long petiole and entire-margined lamina with actinodromous venation, UF 18969-61744. **B**. Obovate leaf with crenate margin, UF 18969-60475. **C**. Ovate leaf with weakly crenate margin, UF 18969-50975. **D**. Enlargement of B showing gland-tipped crenations. **E**–**K**. *Nordenskioeldia borealis*. **E**. Fruiting axis, UF 18969-34519. **F**. Fruit, in lateral view, with dorsal surfaces of four fruitlets exposed, reflected light, UF 18969-61727. **G**. Lateral view of fruitlet on left side of F, surface rendering from CT-scan. **H**. Apical view of the four fruitlets seen in F, μCT surface rendering. **I**. Fruitlet in lateral view, reflected light, UF 18969-34510. **J**, **K**. Enlargements of E. **J**. Persisting central column from which fruitlets have dispersed. **K**. Transverse view of receptacle that has dispersed all fruitlets. Scale bars = 10 mm in A–C, E; 5 mm in F, I–K

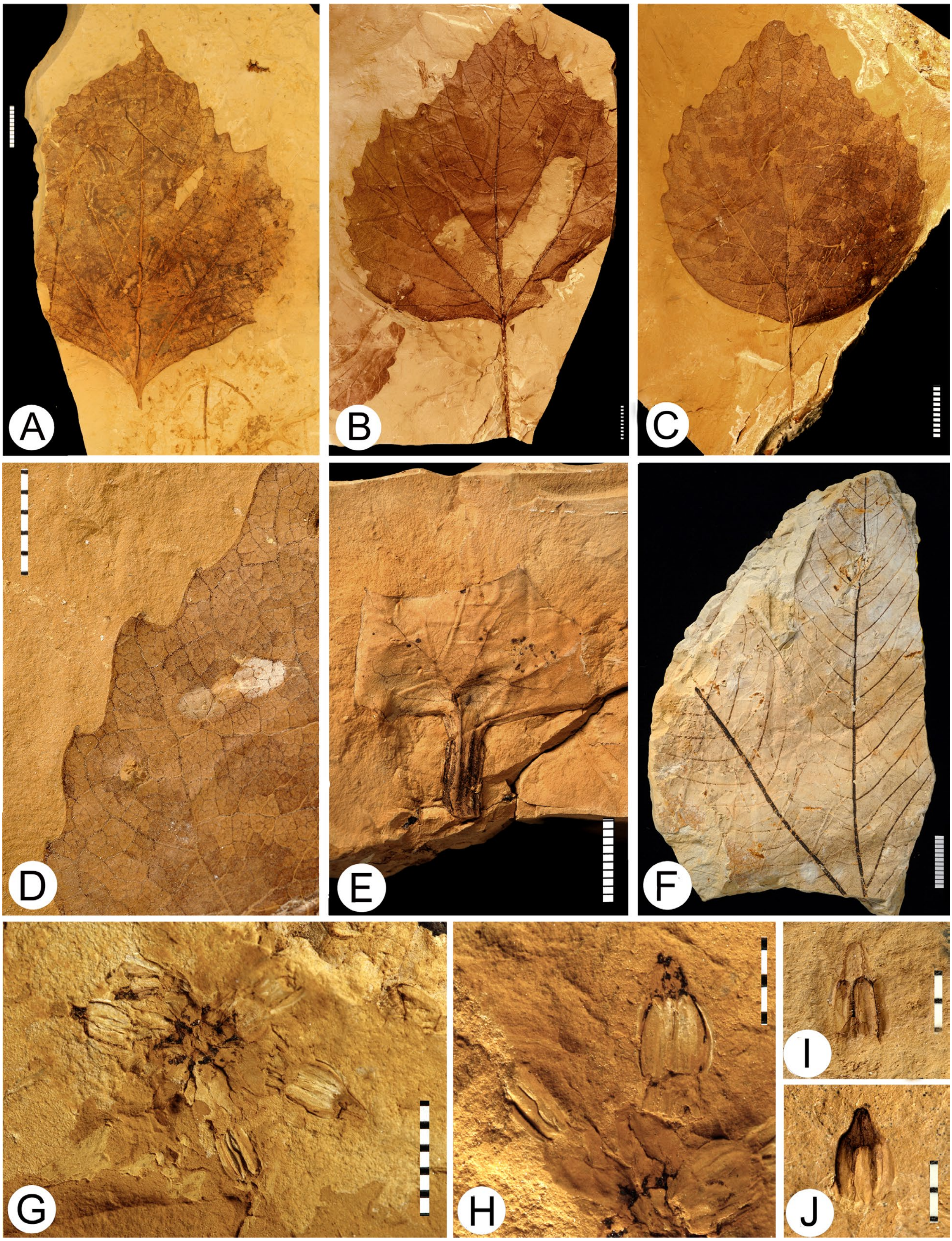

Figure 5. Platanaceae. **A–E**. *Platanus* sp.; **A**. Ovate lamina, UF 18969-34582; **B**. Ovate, weakly lobed lamina on slender petiole, serrated with rounded sinuses between the teeth, UF 18969-34567; **C**, **D**. Ovate lamina with slender petiole, UF 18969-34598; **D**. Enlargement of C, showing glandular teeth and details of venation; **E**. Stipule, UF 18969-34603; **F**. *Macginitiea gracilis* leaf showing two of the usual five lobes, UF 18969-38380; **G–J**. *Macginistemon mikanoides*; **G**. Staminate capitulum, UF 18969-34593; **H**. Enlargement of G, showing protruding stamen group with domed apex; **I**, **J**. Dispersed stamens, UF 18969-34520 and UF 18969-34588b. Scale bars = 9 mm in A; 10 mm in B, C, E, F; 5 mm in D, G; 2 mm in H–J

acute. Lamina 60–120 mm long, 40–85 mm wide. Petioles are long (3 to more than 5 cm) and narrow (~1 mm thick). Margins regularly serrate, with gland-tipped teeth and rounded sinuses. Venation sometimes actinodromous with three primary veins, to pinnate with a single primary vein and strong basal pair of secondary veins, secondary veins craspedodromous. Agrophic veins present, simple. Intercostal tertiary veins opposite percurrent. Higher order venation forming a regular reticulum with good areole development. Stipule with a cylindrical sleeve 12 mm long having several parallel veins that radiate apically into a peltate lamina 3 cm wide with at least eight shallow lobes and craspedodromous major veins.

Specimens examined. UF 18969-34567, 34582, 34595, 34598, 34603, 34606, 61732.

Discussion. A single stipule was recovered which might correspond to the same species (Fig. 5E), resembling those more common at the nearby Black Eagle Canyon site. This *Platanus* species is common at the Horse Creek and Black Eagle Canyon and ranges in length even up to 25 cm. Despite the large size of some of the laminae, the petioles are relatively narrow. We did not observe any scars on the petioles that would indicate them to be possessing lateral leaflets, so we do not think this belongs in the compound leaf species, *Platanites raynoldsii* as summarized by Manchester (2014). These leaves differ from *Macginitiea* by the shallow interlobal sinuses, and lack of the series of chevron-forming secondaries in the axils of diverging primary veins. The associated stipule (Fig. 5E) resembles that of modern species of *Platanus*; such stipules have not been found in direct association with *Platanites* or *Macginitiea*. This species may be in need of a new epithet as these Paleocene North American leaves were traditionally placed in the European Neogene species, *Platanus guillelmae* Goepp. and *P. aceroides* Goepp. (Lesquereux, 1878).

Genus ***Macginitiea*** J. Wolfe et Wehr

Macginitiea gracilis
(Lesquereux) J. Wolfe et Wehr
Fig. 5F

Discussion. One fragmentary specimen is recognizable as a digitately lobed leaf of the genus *Macginitiea*. Based on the pattern of venation visible at the base of the lamina, it appears that this was a 5-lobed leaf conforming to the species *M. gracilis* reviewed by Manchester (2014).

Specimen examined. UF 18969-38380.

Genus ***Macginistemon*** Manchester

Macginistemon mikanoides
(MacGinitie) Manchester
Figs 5G–J, 6

Discussion. Pentagonal stamen groups coalescent by their connectives (Manchester, 1986) are found both dispersed (Fig. 5I, J) and intact within capitula (Fig. 5G, H) in the Horse Creek sediments. These correspond morphologically to those found in association with *Macginitiea* leaves at other Paleocene and Eocene localities of western North America (Manchester, 1986, 2014; Pigg and Stockey, 1991). In addition, some specimens show the staminate capitula borne on short side branches of a raceme-like axis (Fig. 6), as documented previously (Pl. 4, figs 1–8 in Pigg and Stockey, 1991; fig. 4.5 in Manchester, 2014).

Specimens examined. UF 18969-34520, 34588b, 34593, 60476B, C, 34589.

Order SAXIFRAGALES
Bercht. et J. Presl

Family CERCIDIPHYLLACEAE Engl.

Genus ***Trochodendroides*** Berry

Trochodendroides genetrix
(Newberry) Manchester
Fig. 7A, B

Basionym.

1868 *Populus genetrix* Newberry; Newberry, p. 64.
1898 *Populus genetrix* Newberry; Newberry, p. 44, pl. 27. fig. 1. See Manchester (2014) for synonymy.

Discussion. Only a few leaves of this iconic Late Cretaceous to Eocene genus were recovered at the Horse Creek locality. It is recognized by ovate shape, finely serrate margin, actinodromous venation, and long petioles (Fig. 7A, B). Although at most localities where this genus occurs, there are also fruits of

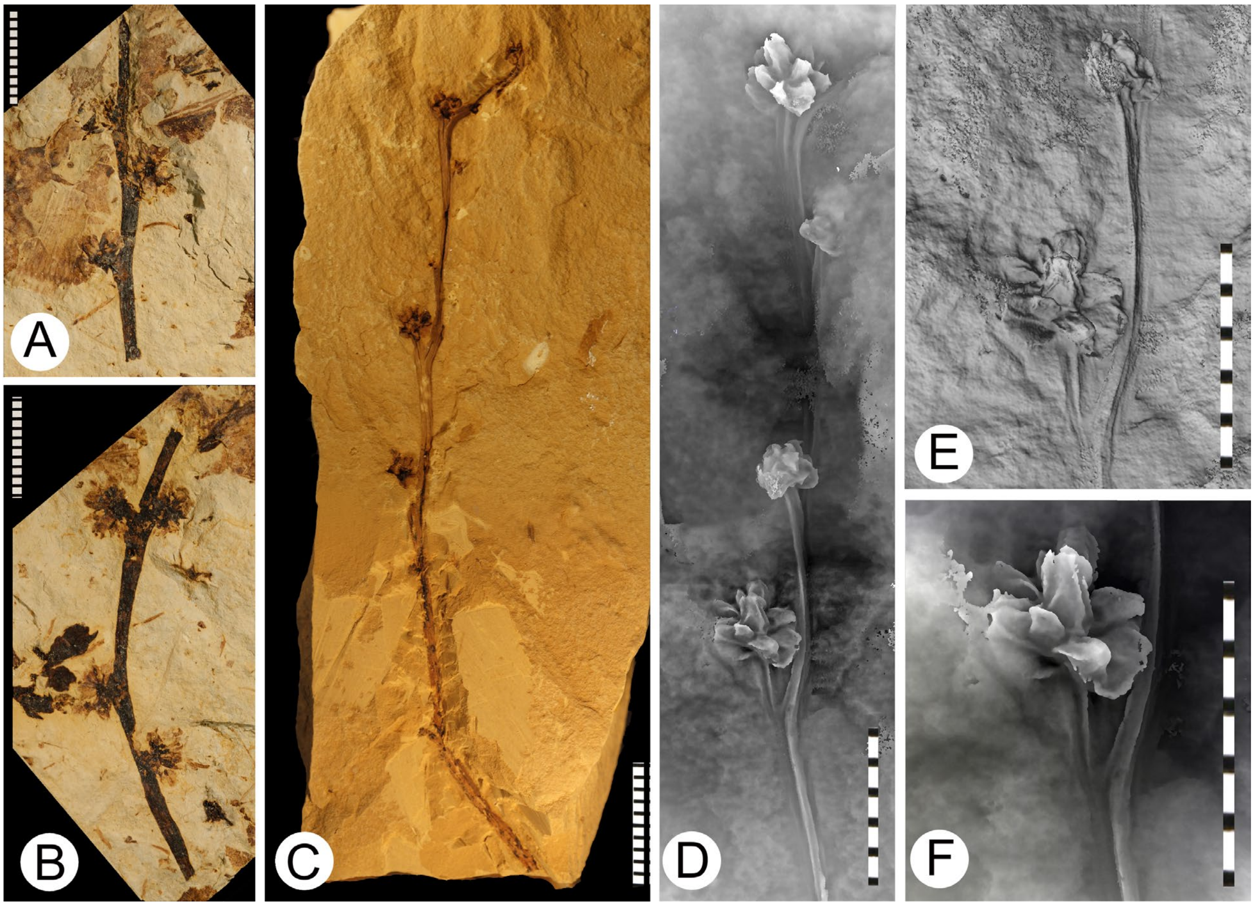

Figure 6. Platanaceous inflorescences of *Macginistemon*. **A**. UF 18969-60476B; **B**. UF 18969-60476C; **C**. Elongate axis with at least four intact capitula, UF 18969-34589; **D–F**. µCT scan of the specimen in C; **D**. Depth map from C showing that capitula are borne on side branches of the main axis; **E**. Surface rendering of lower two capitula of D; **F**. Enlarged capitulum showing stamen groups with domed connectives. Scale bars = 10 mm in A–C; 5 mm in D–F

Jenkinsella, thought to be produced by the same plant (Golovneva and Alekseev, 2017), we did not recover any from this site.

Specimen examined. UF 18969-60476.

Order ROSALES Perleb

Family ULMACEAE Mirb.

Genus ***Ulmites*** J.W. Dawson

Ulmites microphylla (Newberry) Manchester

Fig. 7C–E

Basionym.

1868 *Planera microphylla* Newberry; Newberry, p. 55;
1898 *Planera microphylla* Newberry; Newberry, p. 81, pl. 33, figs 3, 4.

Synonymy.

1977 *Chaetoptelea microphylla* (Newberry) Hickey; Hickey, p. 122.
2014 *Ulmites microphylla* (Newberry) Manchester; Manchester, p. 173, text-fig. 10.

Description. Leaves with ovate lamina having asymmetrical base, and acuminate apex, 23–42 mm long, 14–23 mm wide, with length/width ratios of 1.6:1 to 2.1:1. Petiole short, 2–3 mm, and narrow. Margin serrate, mostly simple nonglandular blunt teeth, but occasionally with subsidiary teeth especially in lower 1/3 of the lamina. Venation pinnate, with 7–11 pairs of straight to sinuous craspedodromous secondary veins. Secondary veins occasionally bifurcating half to two-thirds of the distance to the margin, with each branch directed into a marginal tooth. Veins entering the teeth submedially. Agrophic veins occasionally in lower portion of lamina. Tertiary veins percurrent, opposite to alternate.

Discussion. Leaves of Ulmaceae are recognized by their short, thick petioles and often asymmetrical lamina with serrate margins having teeth that are blunt with the principal vein of each tooth entering submedially. This

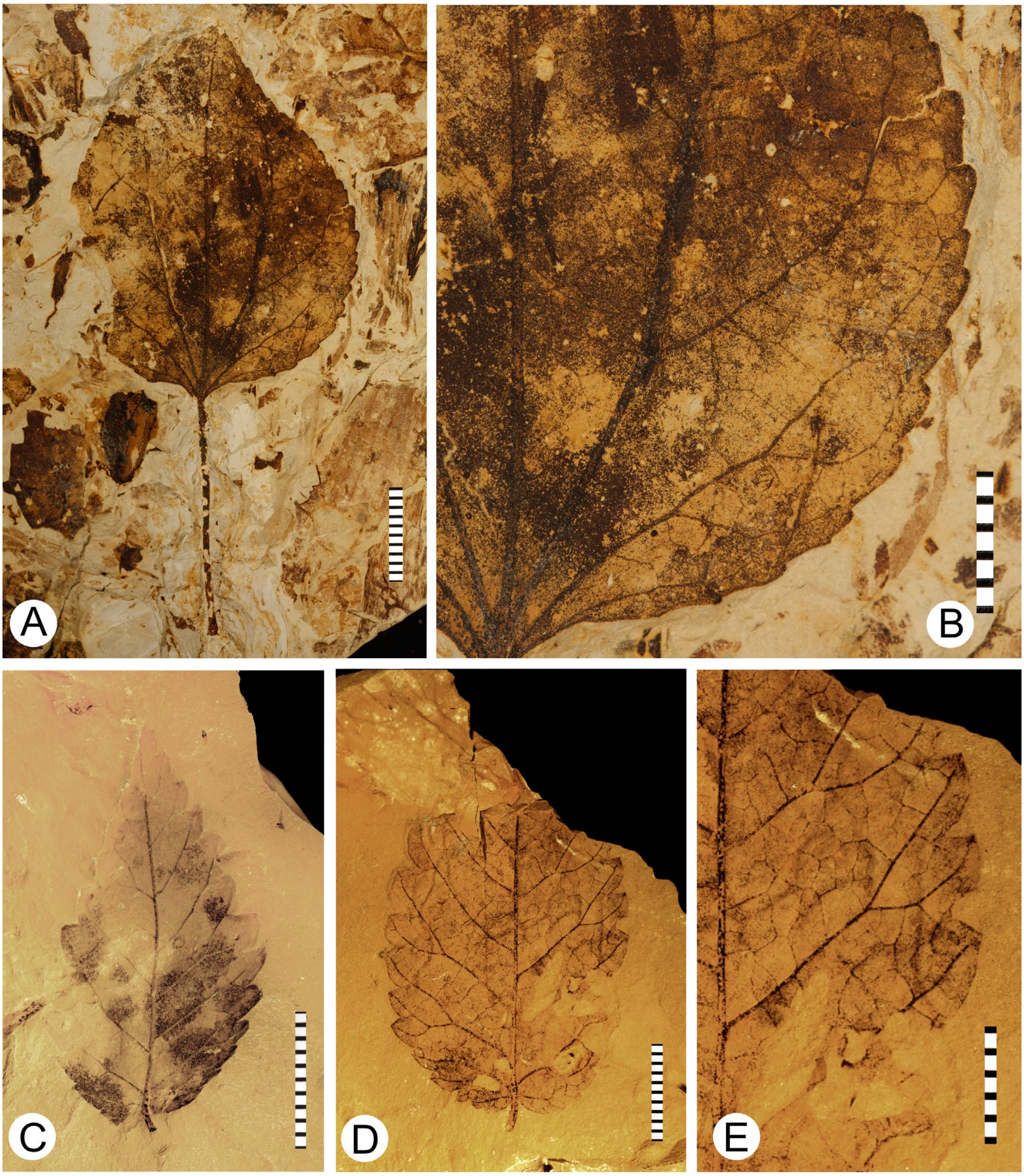

Figure 7. Cercidiphyllaceae and Ulmaceae. **A**. *Trochodendroides genetrix* (Newberry) Manchester leaf with long slender petiole. Finely serrate lamina with actinodromous venation, UF 18969-60476; **B**. Enlargement of A, showing glandular teeth and details of venation; **C–E**. *Ulmites microphylla* leaves; **C**. Small asymmetrical lamina and short thick petiole, UF 18969-38374; **D**. Short, thick petiole, asymmetrical lamina with cordate base, prominent teeth and secondary veins commonly dichotomizing near the margin, UF 18969-34521; **E**. Enlargement of D, showing detail of non-glandular teeth, with submedial vein entry. Scale bars = 10 mm in A, C, D; 5 mm in B, E

leaf form, having one marginal tooth per secondary vein (or two teeth per secondary vein in the case of secondary veins that dichotomize once or twice in route to the margin) closely resembles that of modern *Zelkova* and some *Ulmus*. The fossil genus name *Ulmites* is preferred, however, because the diagnostic fruits of these genera have not been recovered from any Paleocene strata, even though they preserve readily in Eocene and younger sediments (Manchester, 1989, 2014).

Specimens examined. UF 18969-34521, 34536, 34546, 34548, 34551, 34553, 38374, 44615, 60467, 61737.

Order CORNALES Link

Family CORNACEAE Bercht. et J. Presl

Genus ***Cornus*** L.

Cornus swingii
Manchester, Xiang, Kodrul et Akhmetiev
Fig. 8A–C

Discussion. These dogwood leaves are entire-margined with eucamptodromous pinnate secondary veins that curve apically along the margin, accompanied by transverse percurrent tertiary veins (Fig. 8A, B). Fossil leaves from the Horse Creek site were among those used to confirm the identification of *Cornus* leaves in the Paleocene, because they preserve the diagnostic double-armed trichomes as impressions visible under high magnification (Fig. 8C; Manchester et al., 2009).

Specimens examined. UF 18969-34615, 38375.

Family NYSSACEAE Juss. ex Dumort.

Genus ***Davidia*** Baill.

Davidia antiqua (Newberry) Manchester
Figs 8D, E, 9A–C

Discussion. *Davidia* is now endemic to central China, but it was abundant in the Paleocene of North America represented by both leaves and fruits (Manchester, 2002). *Davidia antiqua* is recognizable by its distinctive regularly serrate, cordate-based lamina, long petioles and longitudinally ribbed ellipsoidal fruits at Horse Creek. Permineralized fruits from the Paleocene of North Dakota coincide histologically, as well as morphologically with *Davidia* (Manchester, 2002).

Specimens examined. UF 18969-34527, 34545, 34558, 60472, 61752.

Genus ***Beringiaphyllum***
Manchester, Crane et Golovneva

Beringiaphyllum cupanioides
(Newberry) Manchester, Crane et Golovneva
Fig. 9D, E

Discussion. *Beringiaphyllum* is an extinct leaf type known from the Paleocene of eastern Asia as well as North America (Manchester et al., 1999). It is recognizable by a combination of features including long petioles, lamina that tends to be elliptical and blunt teeth in the upper two-thirds of the lamina. Secondary veins are camptodromous in the lower, entire-margined part of the lamina to craspedodromous in the toothed portion.

Specimen examined. UF 18969-60464.

Genus ***Amersinia***
Manchester, Crane et Golovneva

Amersinia obtrullata
Manchester, Crane et Golovneva
(infructescences and fruits)
Fig. 9F, G

Discussion. *Amersinia* is an extinct genus that was present both in Asia and North America during the Paleocene. The genus consistently co-occurs with *Beringiaphyllum* and is thought to have been produced by the same plant (Manchester et al., 1999). The distinctive obtrulate trilocular fruits are found dispersed in the sediment (e.g. Fig. 9G) and sometimes intact within globose to ellipsoidal infructescences (e.g. Fig. 9F). Permineralized specimens from North Dakota show that they were normally trilocular with one-seed per locule, and an apical germination valve on each carpel (Manchester et al., 1999). These features, along with the lack of a central vascular strand, support assignment to the Nyssaceae.

Specimens examined. UF 18969-34592, 60466.

Genus ***Browniea*** Manchester et Hickey

Browniea serrata
(Newberry) Manchester et Hickey
(leaves and fruits)
Fig. 10

Discussion. *Browniea* is an extinct genus with close similarities to the extant Asian genus *Camptotheca*. It is known from both leaves and fruits that are common in the Paleocene of North America (Manchester and Hickey, 2007). The elongate flattened fruits were borne in globose heads (Fig. 10C). Isolated fruits,

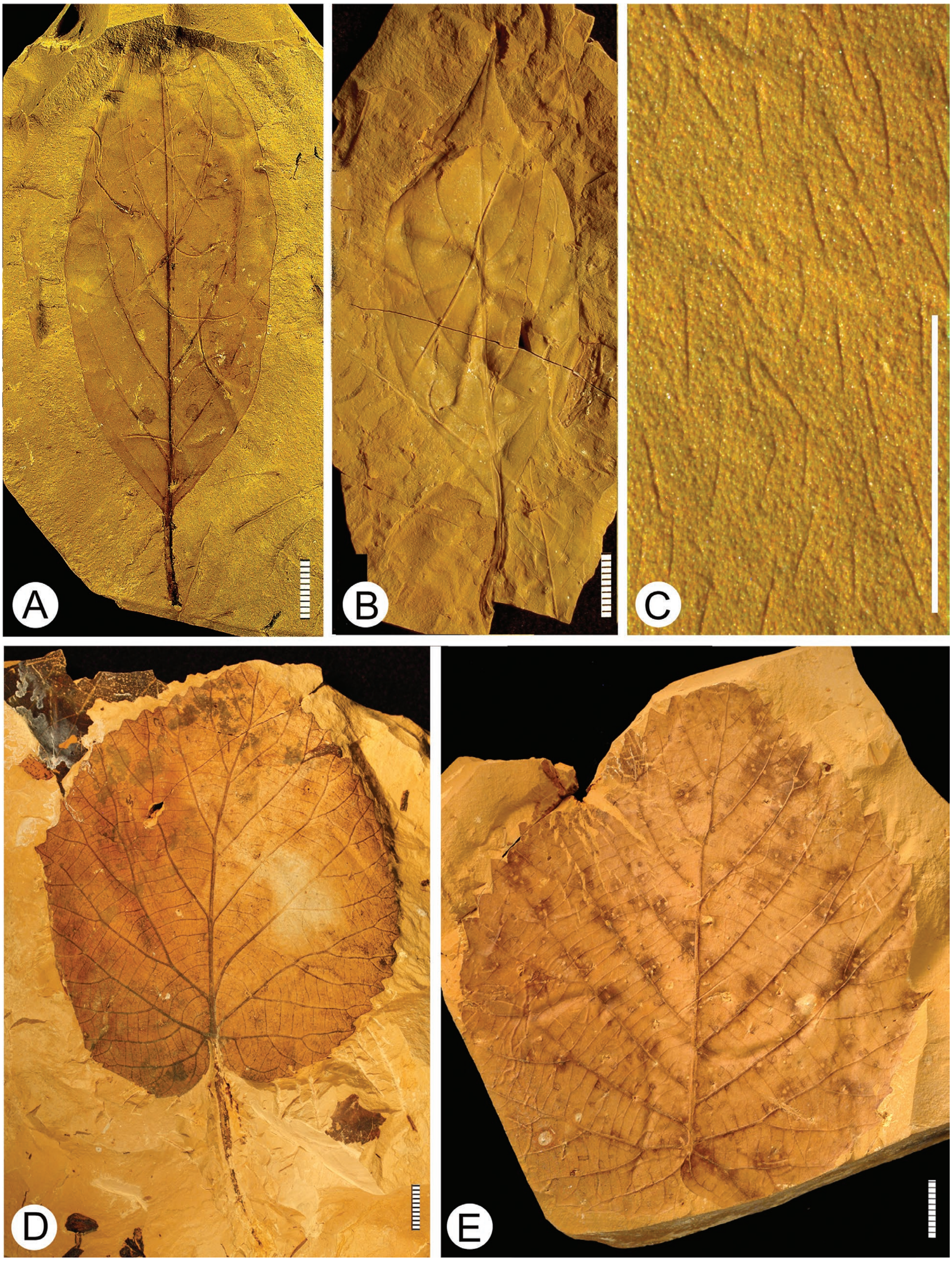

Figure 8. Cornales. **A–C**. *Cornus swingii*. Lamina with entire margins and eucamptodromous venation; **A**, **C**. UF 18969-38375; **B**. UF 18969-34615; **C**. Enlargement of A showing double-armed trichomes; **D**, **E**. *Davidia antiqua*; **D**. Leaf with narrow petiole and serrate lamina with cordate base, UF 18969-60472; **E**. Lamina showing prominent right-angle teeth and pronounced straight, percurrent tertiary veins, UF 18969-34558. Scale bars = 10 mm in A, B, D, E; 1 mm in C

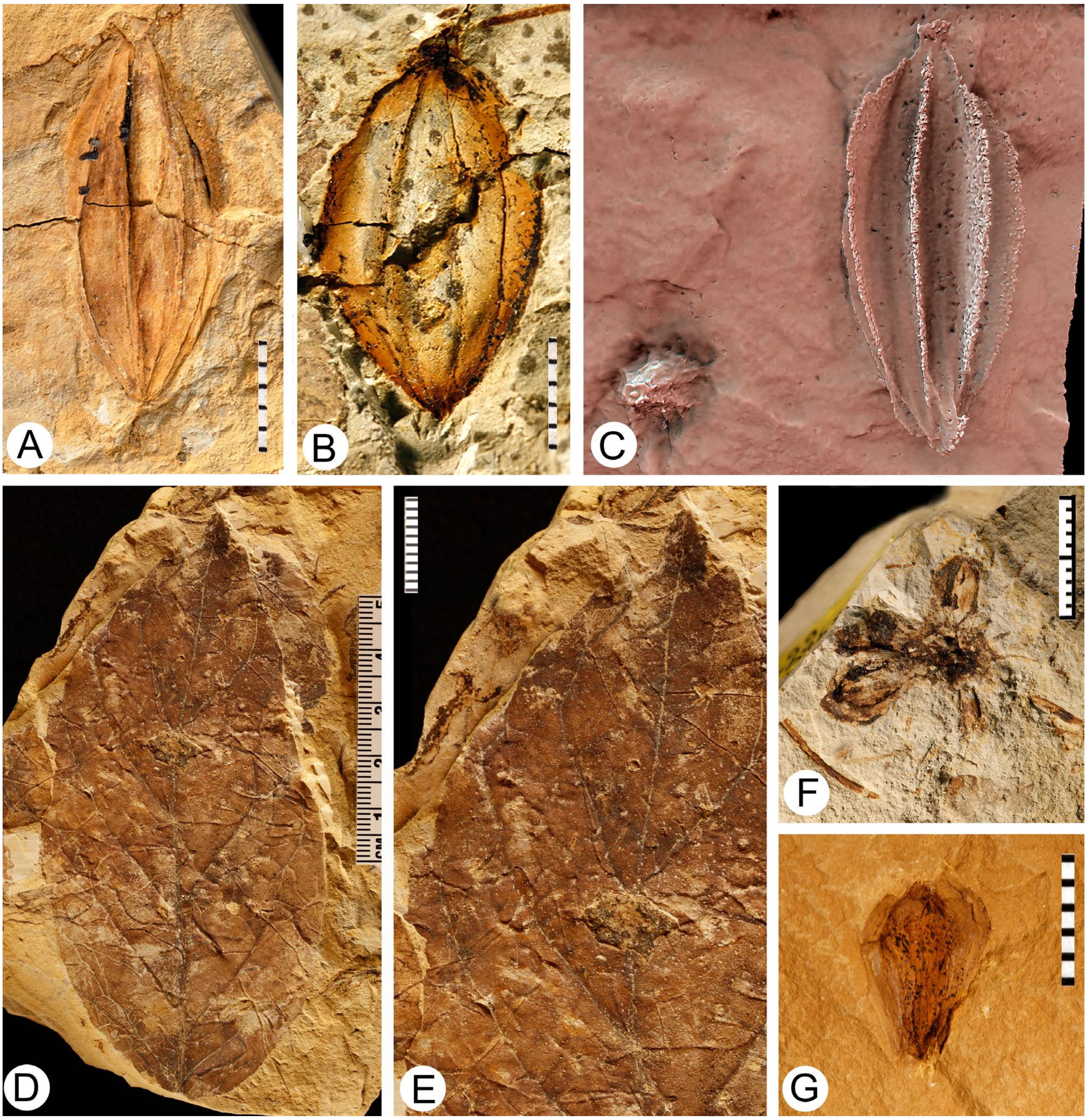

Figure 9. Cornales. **A–C**. Longitudinally ribbed ellipsoidal fruits of *Davidia antiqua*; **A**. UF 18969-34545; **B**. UF 18969-61752; **C**. Two fruits, one in apical view (lower left) and the other in lateral view (right), µCT, UF 18969-34527; **D**, **E**. *Beringiaphyllum cupanioides*. Blunt teeth in the upper two-thirds of the lamina, UF 18969-60464; **F**, **G**. *Amersinia obtrullata* fruits; **F**. Infructescence, UF 18969-60466; **G**. Dispersed fruit, UF 18969-34592. Scale bars = 5 mm in A, B, G (applies also to C); 5 cm in D; 1 cm in E, F

with persistent apical perianth (Fig. 10D), are common and occasional denuded heads (Fig. 10F) from which the fruits were shed are found as well. The leaves, found in close association at more than 30 localities in Colorado, Wyoming, Montana, North Dakota, Alberta and Saskatchewan (Manchester and Hickey, 2007), are elliptical, ovate, or rarely obovate, nearly symmetrical, commonly with marginal teeth (Fig. 10A, B).

S p e c i m e n s   e x a m i n e d. UF 18969-34492, 34498, 34516, 50984, 60469, 61734.

Order SAPINDALES
Juss. ex Bercht. et J. Presl

Family SAPINDACEAE Juss.

Genus ***Aesculus*** L.

Aesculus hickeyi Manchester
(leaves and fruit pieces)

Fig. 11

D i s c u s s i o n. Complete palmately compound leaves of the horse chestnut, *Aesculus hickeyi,*

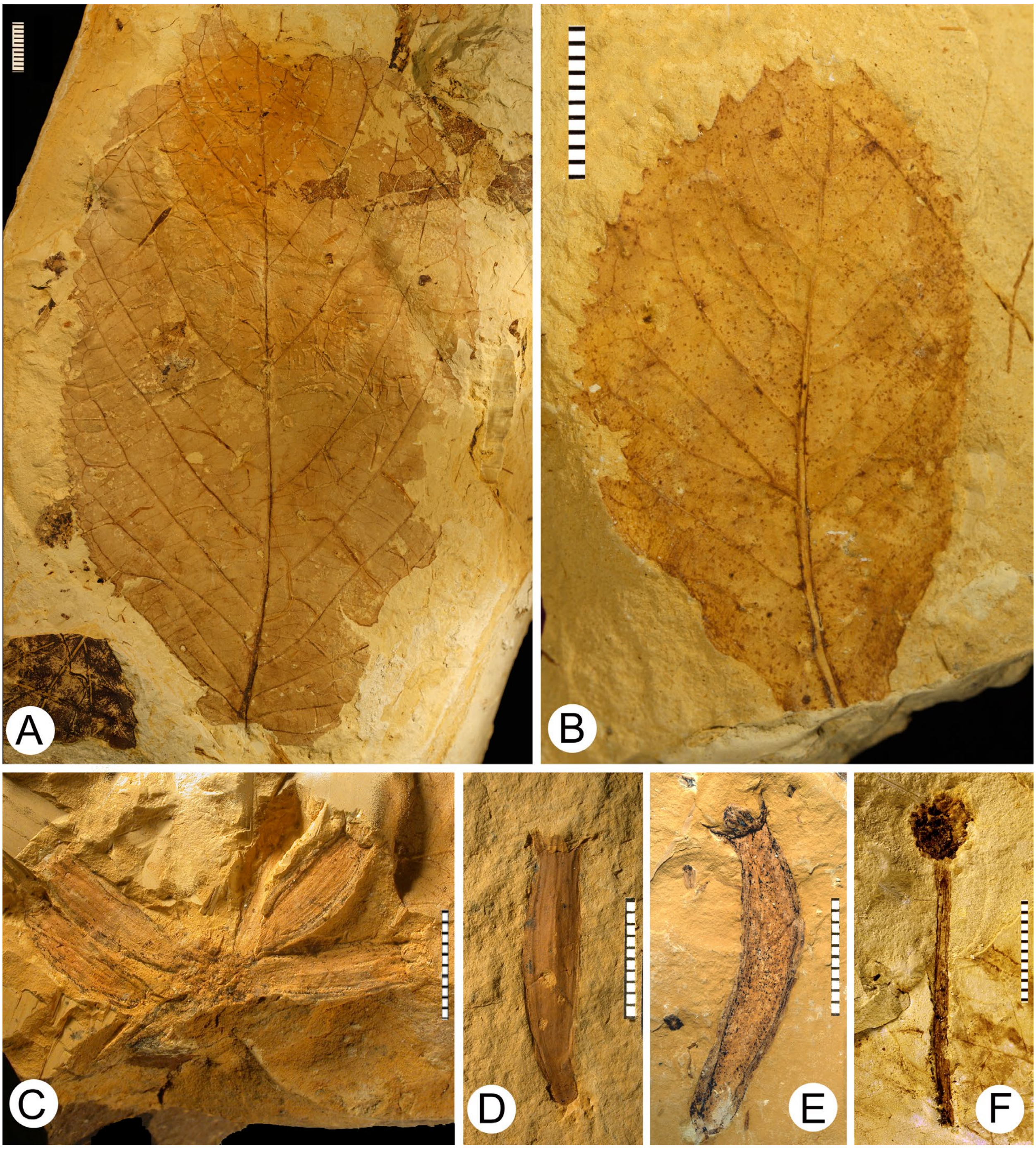

Figure 10. Cornales *Browniea serrata*. **A**, **B**. Leaves; **A**. UF 18969-60469; **B**. UF 18969-61734; **C–E**. Elongate flattened fruits. **C**. Fruits borne in globose head, UF 18969-34516; **D**, **E**. Isolated fruits with persistent apical perianth; **D**. UF 18969-34498; **E**. UF 18969-50984; **F**. denuded head from which the fruits were shed, UF 18969-34492. Scale bars = 10 mm in A–F

have been recovered from several Paleocene North American sites in association with distinctive fruiting remains (Manchester, 2001). At Horse Creek, only a few isolated leaflets (Fig. 11B, C), a partial compound leaf (Fig. 11A), and several fragmentary fruit capsule remains (Fig. 11D–H) and probable seeds (Fig. 11I–K) have been recovered. The ovate leaflets are recognized by their cuneate bases, evenly pinnate, mostly craspedodromous, occasionally semicraspedodromous secondary veins, and finely serrate margins. Although the isolated leaflets were for many years confused with those of Juglandaceae and misidentified to the species *Carya antiquorum* Newberry (e.g., Brown, 1962; Hickey, 1977, 1980), they differ in lamina shape, prominence of tertiary veins, and serration from the type material of *C. antiquorum* which indeed belongs to the Juglandaceae (Manchester, 2001).

Specimens examined. UF 18969-34564, 34566, 34608, 34569, 38373, 38384, 38369, 50982.

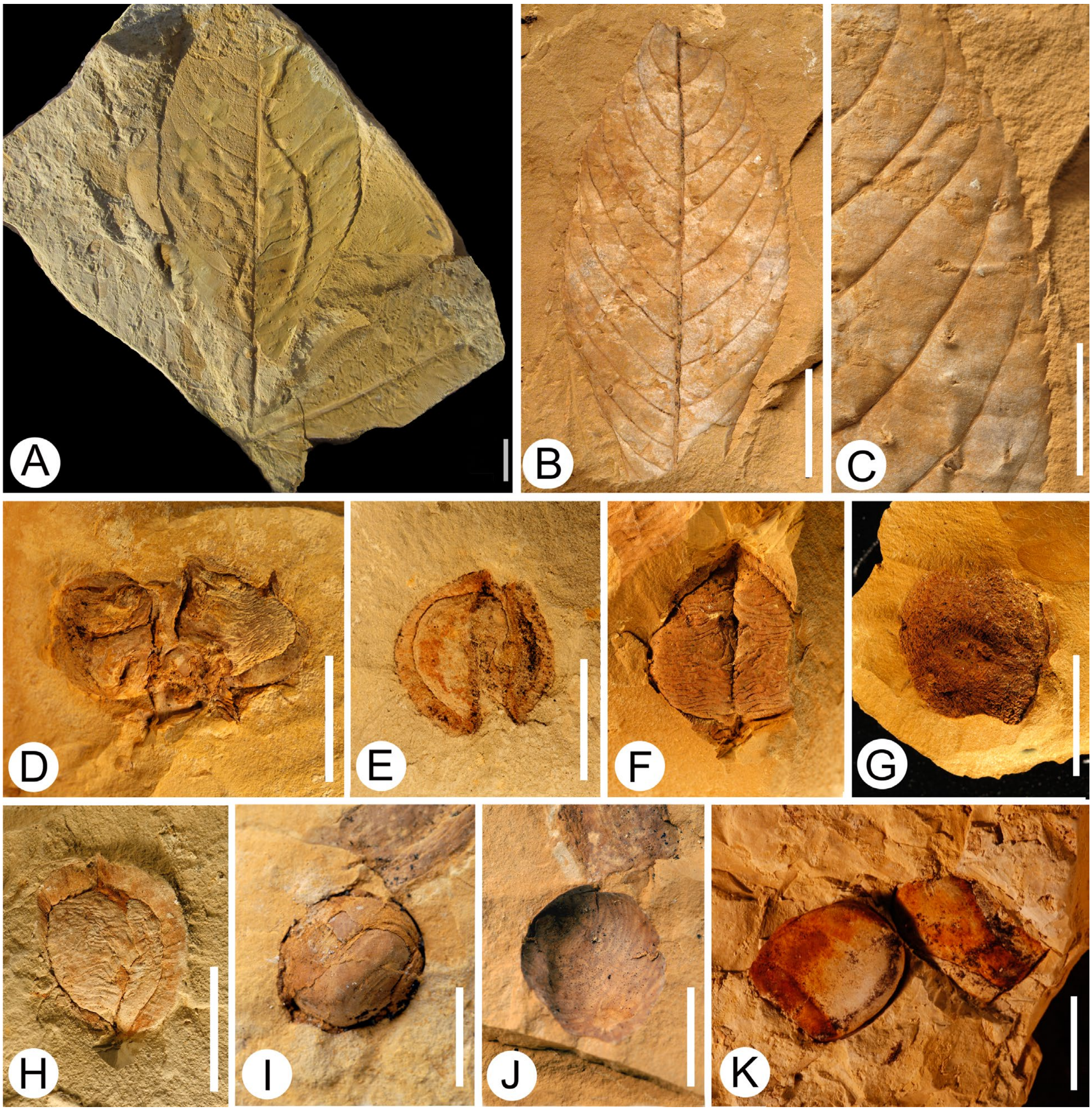

Figure 11. *Aesculus hickeyi*. **A**. Compound leaf showing portions of three leaflets (a fifth one inferred from symmetry), UF 18969-34569; **B**, **C**. Leaflet, UF 18969-38373; **D**–**K**. Fruit remains; **D**. Oblique-apical view of fruit with three valves, UF 18969-34564; **E**. Isolated fruit valve with median septal groove, UF 18969-38384; **F**. Fruit valve, ventral view, with median groove representing the septum, UF 18969-34566; **G**. Counterpart of F, showing the rough-textured external surface of the valve, UF 18969-34566; **H**. Fruit valve, UF 18969-38369; **I**–**K**. Seeds; **I**. Seed cast, UF 18969-34608; **J**. Counterpart of I, seed mold showing smooth external surface, UF 18969-34608; **K**. UF 18969-50982. Scale bars = 10 mm in A–H; 5 mm in I–K

Family cf. RUTACEAE

Genus ***Porosia*** Hickey

Porosia verrucosa (Lesquereux) Hickey emend. Manchester et Kodrul

Fig. 12

Basionym.

1878 *Carpites verrucosus* Lesquereux; Lesquereux, p. 305, Pl. 10, fig. 9.

Synonymy.

1977 *Porosia verrucosa* (Lesquereux) Hickey; Hickey p. 114, pl. 54, figs 1, 3, 4 (not 2).

Discussion. These distinctive reniform, punctate fruits are particularly common in the Paleocene of western North America and eastern Asia. Anatomically preserved specimens indicate that they were single-seeded with a wall containing regularly spaced cavities (Manchester and Kodrul, 2014). Specimens were previously figured from the Horse Creek

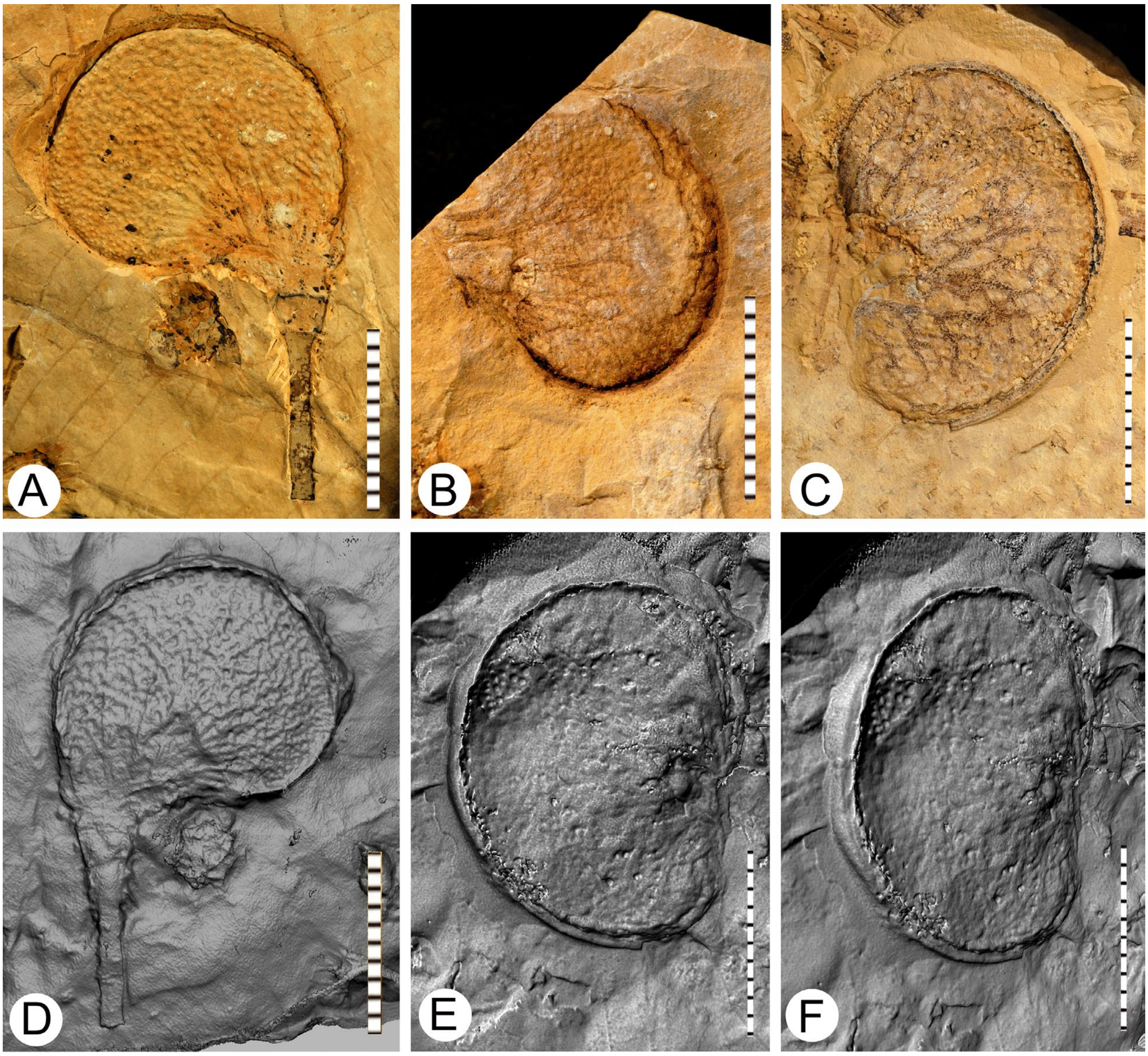

Figure 12. *Porosia verrucosa* fruits. **A**, **D**. UF 18969-61747; **B**. UF 18969-34520; **C**. Fruit showing the reticulate venation pattern, UF 18969-34526; **D**. Surface rendering of the specimen in A, µCT; **E**, **F**. Surface rendering of the specimen in C, in lateral (E) and oblique-tilted view (F), to show smooth dorsal and lateral surfaces, with part of the exocarp removed showing circular tubercles. Scale bars = 10 mm

florule (Pl. 2, figs 5, 6, 9 in Manchester and Kodrul, 2014). Here we figure additional specimens by reflected light and µCT scan, including a pedunculate specimen showing scars of the hypogynous perianth (Fig. 12A, D).

Specimens examined. UF 18969-34520, 34526, 61747.

Family Indet.

Genus ***Phyllites*** Brongniart

Phyllites demoresii Brown

Fig. 13A–F

Description. Lamina elliptic to wide-elliptic to slightly obovate, 5.0–5.6 cm wide and at least 5.8–8.8 cm long, entire-margined, with a rounded, somewhat asymmetrical base and acute apex. Petiole/petiolule long, slender, 5.0 cm long, of consistent thickness without widening at the junction with lamina. Venation pinnate with 5 to 7 secondary veins arising from the midvein at 38–50° angles, the basal pairs arising decurrently from the midvein; secondary veins irregular in course and sometimes sinuous; irregularly spaced, farther apart towards the apex, forming brochidodromous loops at the margin. Intersecondaries occasional. Tertiary veins widely spaced, straight, opposite to sinuous percurrent; quaternary and higher order veins forming quadrangular mesh.

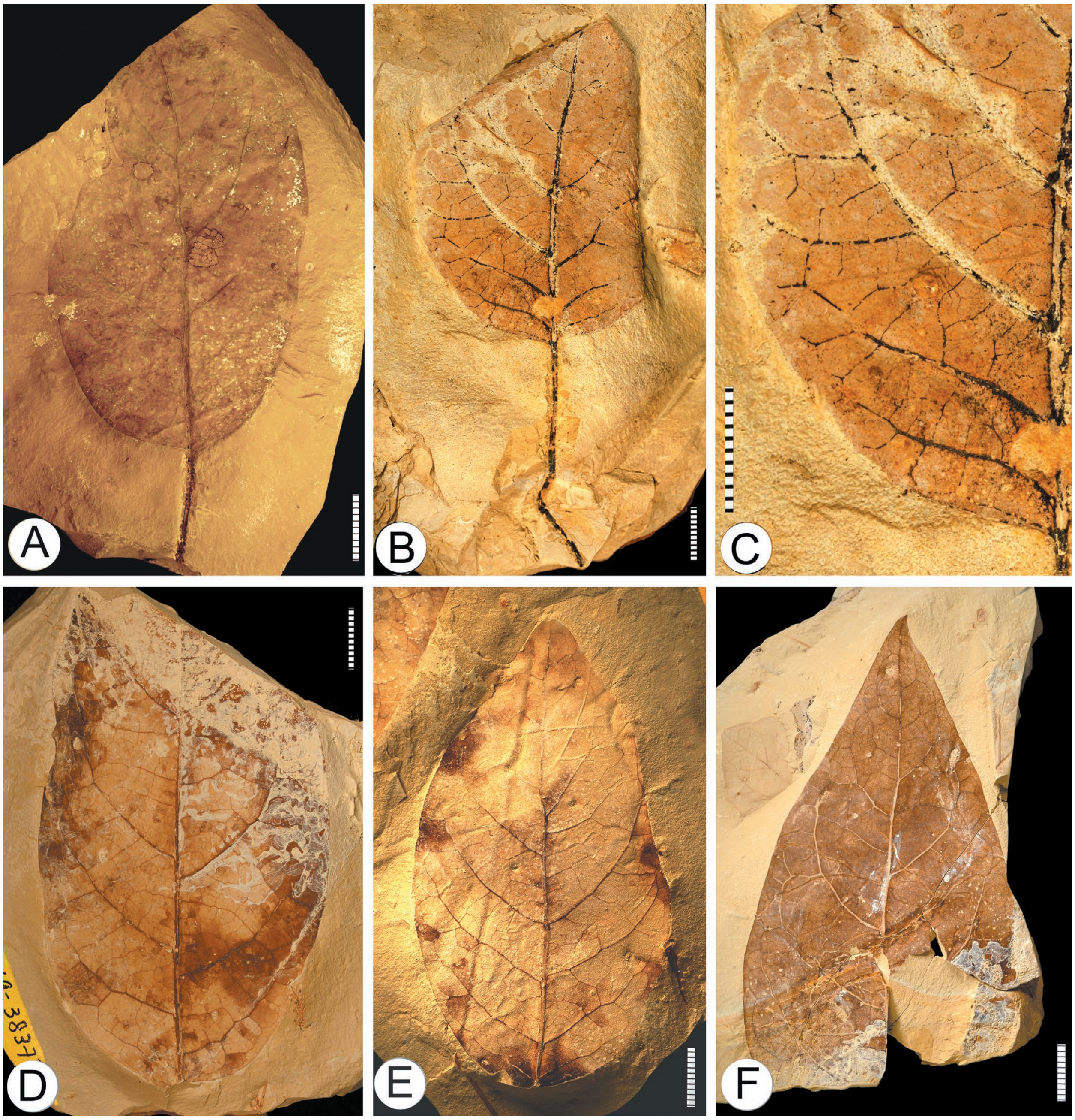

Figure 13. *Phyllites demoresii* Brown. **A**. Entire-margined lamina and long slender petiole, UF 18969-34561; **B**, **C**. Another leaf with long petiole, UF 18969-60462; **D**. UF 18969-38377; **E**. UF 18969-38372; **F**. UF18969-38379

Specimens examined. UF 18969-60462, 34561, 38372, 38377, 38379.

Discussion. These entire-margined leaves with long slender petioles, rounded bases and acuminate apices correspond to those that Brown (1962) named *Phyllites demoresii* from Paleocene sites in Wyoming, Montana and North Dakota. He figured specimens showing the long narrow petiole and noted that the secondaries are widely spaced, forming conspicuous closed loops well within the margin, and that intersecondary veins are common. This leaf type also resembles those called *Nyssa bureica* Krassilov from the late Cretaceous and early Paleocene of the Amur Region, Far Eastern Russia (Krassilov, 1976; Moiseeva et al., 2018). In addition to the features described by Brown (1962), the base of the lamina is slightly asymmetrical, with the blade tissue extending 1 to 2 mm farther down the petiole on one side than the other, possibly an indication that these might be leaflets of a compound leaf. Both in the Far Eastern deposits and in many North American sites, such leaves co-occur with *Porosia* fruits.

CONCLUSIONS

The Horse Creek florule is a relatively low-diversity assemblage of about 16 genera (Table 1) dominated by Cornales (*Cornus*, *Davidia*, *Beringiaphyllum* and *Browniea*), accompanied by frequent Platanaceae (*Platanus*, *Macginitiea*), Ulmaceae (*Ulmites*), occasional Sapindaceae (*Aesculus*), and cupressaceous conifers. The presence of *Taxodium* is consistent with a swampy environment. A fish scale and snail were also recovered from the same site. Although these plants are preserved in clastic siltstone sediment, it is likely that these taxa contributed to the formation of coals like those that are underlying this unit. The Carneyville coal mine florule of northern Wyoming (Li et al., 2018), 73 km SW of Horse Creek, is also low in diversity; all of its angiosperm species are shared with Horse Creek (*Aesculus, Davidia*, *Platanus*, *Trochodendroides, Zizyphoides, Porosia*), but the Cupressaceae is represented by *Glyptostrobus* rather than *Taxodium*.

Many of the species considered here were also recognized by Hickey (1980) in a biostratigraphic and facies analysis of the Paleocene of the Clark Fork basin in the northern part of the Bighorn Basin about 240 km to the west of Horse Creek. Some of the taxa, e.g. *Aesculus hickeyi* (which he called "*Carya*" *antiquorum*), *Trochodendroides genetrix* ("*Cercidiphyllum genetrix*"), *Browniea serrata* ("*Eucommia serrata*") and *Beringiaphyllum cupanioides* ("'*Viburnum*' *cupanioides*"), occur throughout the Paleocene section there, i.e. in Puercan Torrejonian, Tiffanian and Clarkforkian strata. *Porosia* is indicated as stretching from Torrejonian-Clarkforkian, but also with occurrences in the late Cretaceous. Two of the Horse Creek species have first appearances in the Tiffanian in the Clark Fork basin: *Ulmites microphylla* ("*Chaetoptelea microphylla*") and *Davidia antiquum* ("'*Viburnum*' *antiquum*"). Hickey (1980) noted an increase in diversity, possibly representing new immigrants, in the latest Paleocene stage, Clarkforkian. The relatively low diversity of the Horse Creek florule is consistent with Hickey's observation that "the low diversity of the Tiffanian Stage appears to be real and not simply a function of the number of species of localities collected. No locality in this stage has yet yielded more than 11 species even though the number of specimens from localities with this maximum species number ranges from 79 to 257" (Hickey, 1980: p. 46).

The low diversity of Tiffanian floras was also documented by Gemmill and Johnson (1997) in their study of adjacent paleobotanical quarries of the Bison Basin flora in the Great Divide Basin of Wyoming, ~360 km SE. Their team collected 500 or more specimens from each quarry and found taxonomic diversity of only 7 to 15 species per quarry. Some of the taxa known from the Horse Creek florule occur there, as well: *Equisetum*, *Trochodendroides*, *Beringiaphyllum cupanioides* and *Aesculus hickeyi*. Contrary to these observations, the Paleocene lacustrine flora of Almont, North Dakota, which has also been considered Tiffanian in age (Crane et al., 1990; Zetter et al., 2011), has a higher diversity. Crane et al. (1990) recognized 30 different types of fruits and seeds, and 24 kinds of leaves, which could represent as many as 30 to 45 biological species depending on the extent to which the same species are represented by different isolated organs. Crane et al. (1990) surmised that the high apparent diversity of the Almont site might reflect the greater intensity of collecting at the Almont which was actively collected by amateurs seeking *Ginkgo* and other attractive display specimens. However, the diversity of palynomorphs from the same site (more than 50; Zetter et al., 2011) is also higher than expected. It remains possible that Almont is significantly younger. Adjacent radiometric dating is not available and the age was extrapolated with reference to an abstract inferring the age of the Sentinel Butte Formation in that area to be Tiffanian 3 based on freshwater mollusk and mammal correlations (Kihm and Hartman, 1991; Zetter et al., 2011).

The taxonomic diversity at Horse Creek is too low to provide a statistically reliable estimate of paleotemperature and precipitation by means of foliar physiognomy (Peppe et al., 2018). However, the taxonomic composition provides some clues to the climate. All of the woody plants recovered appear to be deciduous based on the habit of their extant relatives (e.g. *Taxodium*, *Platanus*, *Cercidiphyllum*, *Ulmus*, *Cornus*, *Davidia*, *Camptotheca*). This suggests seasonality and a likely temperate or subtropical climate. The distribution of extant *Davidia involucrata* in China is strongly influenced by mean annual temperature which varies from approximately −0.7 to 19.5°C, and by mean annual range of temperature which ranges from approximately 21.9 to 31.9°C (Long et al., 2021). Although mostly temperate today, the 14 extant species of *Aesculus* indicate a wide climatic tolerance for the genus, from temperate to tropical. Du et al. (2020) recorded a range of mean annual temperature varying from 9.9°C. (*A. turbinata*) to 21.6°C (*A. assamica*) and mean annual range of temperature ranging from 18.4°C (*A. assamica*) to 38.5°C (*A. glabra*). *Taxodium* ranges similarly, with temperate populations in the southeastern United States and subtropical to tropical occurrences to southern Mexico and Guatemala (Eckenwalder, 2009). Current data preclude a more precise estimate of the paleoclimate of the Horse Creek florule.

The effort to reconstruct "whole plants" from their isolated organs is easier in floras that are low in diversity. Nearly all of the leaf types present in the Horse Creek florule can be linked to their likely corresponding fruits by their co-occurrence at Horse Creek and many other sites, as well as by clues from shared morphological characters of extant relatives (Table 1). The elliptic, entire-margined leaf with long petiole and pinnate secondary veins of irregular course known as *Phyllites demoresii* Brown from Paleocene sites in Wyoming, Montana and North Dakota (Brown, 1962) has remained uncertain as to its affinities. The extinct genus *Porosia* has also been of uncertain affinity, although a possible relationship with Rutaceae has been suggested (Manchester and Kodrul, 2014), but the coinciding leaves have remained unknown. We have accounted for the affinities of most leaf fossils recovered from the Horse Creek locality; therefore, it seems that *Phyllites demoresii* Brown is the best candidate for the leaf produced by the *Porosia* plant.

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REFERENCES

Barclay, R.S., Johnson, K.R., Betterton, W.J., Dilcher, D.L., 2003. Stratigraphy and megaflora of a K-T boundary section in the eastern Denver Basin, Colorado. Rocky Mountain Geology 38(1), 45–71. https://doi.org/10.2113/gsrocky.38.1.45

Brown, R.W., 1962. Paleocene floras of the Rocky Mountains and Great Plains. United States Geological Survey Professional Paper 375, 1–119.

Bryson, R.P., Bass, N.W., 1973. Geology of Moorhead Coal Field, Powder River, Big Horn, and Rosebud Counties, Montana. United States Geological Survey Bulletin 1338. U.S. Government Printing Office, 116 pages.

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G., 2008. Meshlab, an Open-Source Mesh Processing Tool. In: Scarano, V., De Chiara, R., Erra, U. (eds), Sixth Eurographics Italian Chapter Conference. Geneva: Eurographics Society, pp. 129–136.

Crane, P.R., Manchester, S.R., Dilcher, D.L., 1990. A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota: Fieldiana. Geology Series 20, 1–63.

Crane, P.R., Manchester, S.R., Dilcher, D.L., 1991. Reproductive and vegetative structure of *Nordenskioldia* (Trochodendraceae), a vesselless dicotyledon from the early Tertiary of the Northern Hemisphere. American Journal of Botany 78(10), 1311–1334. https://doi.org/10.1002/j.1537-2197.1991.tb12599.x

Culbertson, W.C., 1987. Diagrams showing proposed correlations and nomenclature of Eocene and Paleocene coal beds in the Birney 30' × 60' quadrangle. Big Horn, Rosebud, and Powder River counties, Montana: United States Geological Survey Coal Investigations Map C-113.

Du, Z.Y., Harris, A.J., Xiang, Q.Y.J., 2020. Phylogenomics, co-evolution of ecological niche and morphology, and historical biogeography of buckeyes, horsechestnuts, and their relatives (Hippocastaneae, Sapindaceae) and the value of RAD-Seq for deep evolutionary inferences back to the Late Cretaceous. Molecular Phylogenetics and Evolution 145, article 106726. https://doi.org/10.1016/j.ympev.2019.106726

Eckenwalder, J.E., 2009. Conifers of the World. Timber Press. Portland, Oregon, 720 pp.

Ellis, B., Johnson, K.R., Dunn, R.E., 2003. Evidence for an in situ early Paleocene rainforest from Castle Rock, Colorado. Rocky Mountain Geology 38(1), 73–100. https://doi.org/10.2113/gsrocky.38.1.173

Ellis B., Daly, D.C., Hickey, L.J., Johnson, K.R, Mitchell, J.D., Wilf, P, Wing S.L., 2009. Manual of leaf architecture. Cornell University Press, Ithaca, NY.

Gemmill, C.E.C., Johnson, K.R., 1997. Paleoecology of a late Paleocene (Tiffanian) megaflora from the northern Great Divide Basin, Wyoming. Palaios 12(5), 439–448. https://doi.org/10.2307/3515382

Golovneva, L.B., Alekseev, P.I., 2017. Taxonomy and morphological diversity of infructescences *Jenkinsella* co-occurred with *Trochodendroides* leaves in the Cretaceous and Paleogene. Paleobotanica 8, 92–121. https://doi.org/10.31111/palaeobotany/2017.8.92

Heer, O., 1868. Die fossile Flora der Polarländer, in Flora fossilis arctica, Band 1: enhaltend die in Nordgrönland, auf der Melville-Insel, im Banksland, am Mackenzie, in Island und in Spitzbergen endeckten fossilen Pflanzen. Friedrich Schulthess, Zürich, pp. 1–192.

Hickey, L.J., 1973. Classification of the architecture of dicotyledonous leaves. American Journal of Botany 60, 17–33. https://doi.org/10.1002/j.1537-2197.1973.tb10192.x

Hickey, L.J., 1977, Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of Western North Dakota. Geological Society of America Memoir 150, 1–183.

Hickey, L.J., 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin. Early Cenozoic paleontology and stratigraphy of the Bighorn basin, Wyoming. Univ. Michigan Papers in Paleontology 24, 33–49.

Huegele, I.B., Manchester, S.R., 2020. An Early Paleocene carpoflora from the Denver Basin of Colorado, USA, and its implications for plant-animal interactions and fruit size evolution. International Journal of Plant Sciences 181(6), 646–665. https://doi.org/10.1086/707727

Huegele, I.B., Manchester, S.R., 2022. The mid-Paleocene fruit and seed flora from the Fort Union Formation of Newell's Nook, southeastern Montana, USA. Acta Palaeobotanica 62(2), 93–107. https://doi.org/10.35535/acpa-2022-0009

Husby, C., 2013. Biology and functional ecology of *Equisetum* with emphasis on the giant horsetails. The Botanical Review 79(2), 47–177. https://doi.org/10.1007/s12229-012-9113-4

Kihm A.J., Hartman J.H., 1991. The age of the Sentinel Butte Formation, North Dakota. Journal of Vertebrate Paleontology 11, 40A (abstract).

Krassilov, V.A., 1976. Tsagayan flora of the Amur Region. Nauka Moscow, 92 pp., 43 pls.

Lesquereux, L., 1878. Contributions to the flora of the Western Territories II. The Tertiary flora. Report of the U. S. Geological Survey of the Territories 7, 1–366.

Li, L., Jin, J.H., Manchester, S.R., 2018. Cupressaceae fossil remains from the Paleocene of Carneyville, Wyoming. Review of Palaeobotany and Palynology 251, 1–13. https://doi.org/10.1016/j.revpalbo.2017.12.003

Long, T., Tang, J., Pilfold, N.W., Zhao, X., Dong, T., 2021. Predicting range shifts of *Davidia involucrata* Ball. under future climate change. Ecology and Evolution 11(18), 12779–12789. https://doi.org/10.1002/ece3.8023

Manchester, S.R., 1986. Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of Western North America. Botanical Gazette 147(2), 200–226.

Manchester, S.R., 1989. Systematics and fossil history of the Ulmaceae. Evolution, systematics, and fossil history of the Hamamelidae. In: Crane, P.R., Blackmore, S. (Eds), Evolution, Systematics, and fossil history of the Hamamelidae, Volume 2: 'Higher' Hamamelidae, Systematics Association Special Volume no. 40B, Clarendon Press, Oxford, pp. 221–251.

Manchester, S.R., 2001. Leaves and fruits of *Aesculus* (Sapindales) from the Paleocene of North America. International Journal of Plant Science 162(4), 985–998. https://doi.org/10.1086/320783

Manchester, S.R., 2002. Leaves and fruits of *Davidia* (Cornales) from the Paleocene of North America. Systematic Botany 27(2), 368–382. https://doi.org/10.1043/0363-6445-27.2.368

Manchester, S.R., 2014. Revisions to Roland Brown's North American Paleocene Flora. Acta Musei Nationalis Pragae 70(3–4), 153–210. https://doi.org/10.14446/AMNP.2014.153

Manchester, S.R., Hickey, L.J., 2007. Reproductive and vegetative organs of *Browniea* gen. n. (Nyssaceae) from the Paleocene of North America. International Journal of Plant Sciences 168(2), 229–249. https://doi.org/10.1086/509661

Manchester, S.R., Kodrul, T.M., 2014. Morphology, affinities and phytogeographic history of *Porosia* Hickey in the Cretaceous and Paleocene of North America and Asia. Acta Palaeobotanica 54(1), 77–99. https://doi.org/10.2478/acpa-2014-0002

Manchester, S.R., Crane, P.R., Golovneva, L., 1999. An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and Eastern Asia. International Journal of Plant Science 160, 188–207. https://doi.org/10.1086/314114

Manchester, S.R., Xiang, Q.Y., Kodrul, T.M., Akhmetiev, M.A., 2009. Leaves of *Cornus* (Cornaceae) from the Paleocene of North America and Asia confirmed by trichome characters. International Journal of Plant Sciences 170(1), 132–142. https://doi.org/10.1086/593040

McIver, E.E., Basinger, J.F., 1993. Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. Palaeontographica Canadiana 10, 1–167.

Moiseeva, M.G., Kodrul, T.M., Herman, A.B., 2018. Early Paleogene Boguchan flora of the Amur Region (Russian Far East): composition, age and palaeoclimatic implications. Review of Palaeobotany and Palynology 253, 15–36. https://doi.org/10.1016/j.revpalbo.2018.03.003

Newberry, J.S., 1868. Notes on the later extinct floras of North America, with descriptions of some new species of fossil plants from the Cretaceous and tertiary strata. Annals of the Lyceum of Natural History of New York 9, 1–76.

Newberry, J.S., 1898. The later extinct floras of North America. Monographs of the United States Geological Survey 35, 1–295, 68 pls.

Peppe, D.J., 2010. Megafloral change in the early and middle Paleocene in the Williston Basin, North Dakota, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 298(3–4), 224–234. https://doi.org/10.1016/j.palaeo.2010.09.027

Peppe, D.J., Johnson, K.R., Evans, D.A., 2011. Magnetostratigraphy of the Lebo and Tongue River Members of the Fort Union Formation (Paleocene) in the northeastern Powder River Basin, Montana. American Journal of Science 311(10), 813–850. http://dx.doi.org/10.2475/10.2011.01

Peppe, D.J., Baumgartner, A., Flynn, A., Blonder, B., 2018. Reconstructing paleoclimate and paleoecology using fossil leaves. In: Croft, D.A. et al. (eds), Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities, Vertebrate Paleobiology and Paleoanthropology. Methods in paleoecology, Springer, pp. 289–231.

Pigg, K.B., DeVore, M.L., 2010. Floristic composition and variation in late Paleocene to early Eocene floras in North America. Bulletin of Geosciences 85(1), 135–154. http://dx.doi.org/10.3140/bull.geosci.1136

Pigg, K.B., Stockey, R.A., 1991. Platanaceous plants from the Paleocene of Alberta, Canada. Review of Palaeobotany and Palynology 70(1–2), 125–146. https://doi.org/10.1016/0034-6667(91)90082-E

Pigg, K.B., DeVore, M.L., Greenwood, D.R., Sundue, M.A., Schwartsburd, P., Basinger, J.F., 2021. Fossil Dennstaedtiaceae and Hymenophyllaceae from the early Eocene of the Pacific Northwest. International Journal of Plant Sciences 182(9), 793–807. https://doi.org/10.1086/715633

Pocknall, D.T., Flores, R.M., 1987. Coal palynology and sedimentology in the Tongue River Member, Fort Union Formation, Powder River Basin, Wyoming. Palaios 2(2), 133–145. https://doi.org/10.2307/3514641

Robinson, L.N., Honey, J.G., 1987. Geologic setting of a new Paleocene mammal locality in the Northern Powder River Basin, Montana. Palaios 2(1), 87–90.

Wang, Y.H., Ferguson, D.K., Feng, G.P., Wang, Y.F., Zhilin, S.G., Li, C.S., Popova-Tselenkova, S., Yang, J., Ablaev, A.G., 2009. The phytogeography of the extinct angiosperm *Nordenskioeldia* (Trochodendraceae) and its response to climate changes. Palaeogeography, Palaeoclimatology, Palaeoecology 280(1–2), 183–192. https://doi.org/10.1016/j.palaeo.2009.05.019

West, C.K., Reichgelt, T., Basinger, J.F., 2021. The Ravenscrag Butte flora: Paleoclimate and paleoecology of an early Paleocene (Danian) warm-temperate deciduous forest near the vanishing inland Cannonball Seaway. Palaeogeography, Palaeoclimatology, Palaeoecology 576, article 110488. https://doi.org/10.1016/j.palaeo.2021.110488

Zetter, R., Farabee, M.J., Pigg, K.B., Manchester, S.R., DeVore, M.L., Nowak, M.D., 2011. Palynoflora of the late Paleocene silicified shale at Almont, North Dakota, USA. Palynology 35(2), 179–211. https://doi.org/10.1080/01916122.2010.501164

Zolina, A.A., Manchester, S.R., Golovneva, L., 2021. Typification of the genus *Zizyphoides* Seward et Conway (Magnoliophyta, Trochodendraceae). Acta Palaeobotanica 61(2), 123–135. https://doi.org/10.35535/acpa-2021-0007