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Fossil leaves, flowers and fruits from the Late Paleocene of Birney, southeast Montana, USA

EMILY WILDER[1] and STEVEN R. MANCHESTER[1*]

[1]Florida Museum of Natural History, University of Florida, Gainesville, FL., 32611-7800, USA; e-mails: wilderemily1@gmail.com, ORCID: 0009-0006-1078-8331; steven@flmnh.ufl.edu, ORCID: 0000-0003-0238-7977

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ABSTRACT. A new Paleocene megafossil plant assemblage is described from the Tongue River Member of the Fort Union Formation of southeastern Montana. Although intensively collected and represented by about 250 specimens, the florule is low in diversity with only 11 species of leaves. Co-occurring flowers and fruits provide additional evidence for reconstructing the plants. Common elements of the florule include *Davidia antiqua*, *Aesculus hickeyi*, *Zizyphoides flabella*, and *Porosia verrucosa*. The florule lacks conifer remains, includes one fern, and is dominated by deciduous angiosperms belonging to genera that were widespread across the northern hemisphere during the Paleocene. In addition, six new angiosperm genera are recognized, including leaves of *Arthayesia* and *Birneyphyllum*, flowers of *Maniastrum* and *Kodrulia*, and fruits of *Linguaflumenia* and *Jinjianhuaia*.

KEYWORDS: Fort Union Formation, Tongue River Member, paleobotany, megafossils, deciduous leaves

INTRODUCTION

Megafossil plants preserved in Paleocene sediments of western North America provide insights into the vegetation, climate and environment that followed the Cretaceous-Paleogene asteroid impact but preceded the peak warming at the Paleocene-Eocene boundary. The Fort Union Formation in southeastern Montana, USA, is rich in fossil plants (Brown, 1962; Manchester, 2014) but only a few sites have been documented in detail. A previous analysis of the Horse Creek florule in the Tongue River Member of the Fort Union Formation documented a relatively low-diversity assemblage adjacent to coal seams which was dominated by *Cornus* L., *Davidia* Baill., *Browniea* Manchester et Hickey, and *Platanus* L. (Manchester et al., 2023). Here we focus on the Birney florule from a somewhat older site also in the Tongue River Member, about 30 km west of the Horse Creek site.

In documenting this fossil assemblage, inferred to be of Late Paleocene (Tiffanian) age, we wished to learn more about site-to-site variation in floristic composition of the Tongue River Member of the Fort Union Formation. It is also of biogeographic interest to compare and contrast this plant community with those known from Paleocene sites in other areas of North America (e.g. Brown, 1962; McIver and Basinger, 1993; Hoffman and Stockey, 2000; West et al., 2021) and around the northern hemisphere. We follow the tradition of emphasizing the fossil leaves that predominate among the megafossils at the site, but we also give special attention to the collection and analysis of co-occurring flowers, fruits and seeds with the eventual goal of understanding which of the newly presented reproductive structures coincided with particular leaf types. By linking the leaves with flowers and/or fruits borne by the same plants, we can gain a more holistic understanding of the botanical relationships of the parent plants (Kvaček, 2008; Manchester et al., 2014).

* Corresponding author

MATERIALS AND METHODS

The fossils were collected from a road cut on the north side of the village of Birney, Montana, on the east side of Tongue River road in siltstones of the Tongue River Member of the Fort Union Formation at 45°19.53384′N, 106°30.49632′W (Figs 1, 2), during one-day visits in the summers of 2002, 2003, 2007, 2008, 2011, 2013, 2014 and 2021 to 2024. The productive shale lenses occur high in the steep road cut, so that each year large pieces weather out and tumble to lower parts of the exposure where they can be split to expose abundant leaves, occasional flowers and fruits. Due to the abundance of leaves at this site, more commonly encountered taxa, such as *Zizyphoides*, *Davidia*, *Aesculus*, and *Arthayesia*, were selectively collected (with fragmentary, weathered, or less well-preserved specimens left behind in the field), retaining the best preserved specimens for the museum collection. Hence, the museum collection is biased in favor of rarer species, but the more common taxa remain quantitatively dominant in the collection. Reproductive remains (flowers, fruits and seeds) are relatively rare in the sediments, so we collected all that were encountered.

The Birney area was included in geologic mapping by Mapel (1976) with his stratigraphic columns 33, 34, 36 intercepting a local coal indicated as being 95 ft (29 m) below the Odell coal bed, an equivalent of the Brewster-Arnold coal bed (Bass, 1924; Mapel et al., 1978). This places the Birney plant bed horizon about 30 m above the Knobloch coal bed and about 140 m below the strata yielding the Horse Creek florule (Manchester et al., 2023).

The precise age of these beds within the Paleocene has not been established locally, but the Tongue River Member has been estimated to range from 62.8 to 61.5 Ma in sediments exposed at Signal Butte near Miles City, ~130 km to the north-northeast (Peppe et al., 2011). The Newells Nook vertebrate fauna and associated fruit and seed flora from the level of the lowest coal of the Tongue River Member on the western edge of the Powder River Basin, 60 km northwest of Birney, was considered to be lower Tiffanian North American Land Mammal Age, or ~60 Ma (Robinson and Honey, 1987; Huegele and Manchester, 2022). These are indications that the Birney florule likely represents the Tiffanian stage of the Late Paleocene. Specimens are housed in the paleobotanical collection of the Florida Museum of Natural History at the University of Florida (catalog numbers prefixed UF). The Birney florule collection includes about 250 specimens, including eleven leaf types, two flower types, and several fruit types.

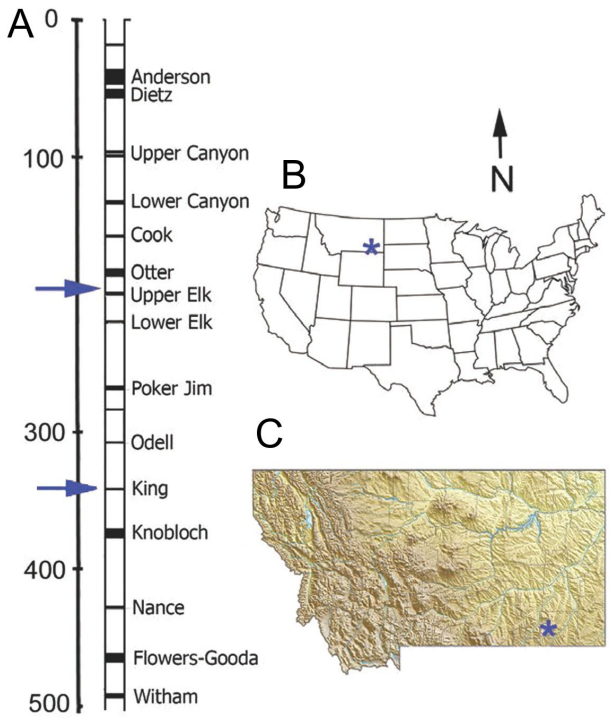

Figure 1. Stratigraphic column (A) for Birney region (B, C), with the Birney site indicated by the lower arrow and Horse Creek by the upper arrow

Photographs of the fossils were taken using a Canon XSi digital camera and an EF-S 60 mm macro lens. Multiple forms of lightning were used depending on the contrast of the specimen. Gooseneck table lamps provided adjustable light direction, and a Dolan-Jenner Fiber-Lite Mi-150 with a linear fiber optic light guide attached allowed for low oblique lighting, which was particularly useful for highlighting faint details in venation in low-contrast specimens. A Keyence VHX-7000N digital microscope was utilized to obtain high-detail images of specimens, with simulated shadow effect illumination and image stitching capabilities.

Fruits and flowers were also investigated using micro-computed tomography (μCT) to document morphological features hidden from optical viewing by overlying sediment. We used a GE Phoenix V|tome|xm240 CT scanner at the University of Florida College of Engineering Nanoscale Research Facility. Voltage was set at 220 kV, and current at 140 μA, and 2100 images, at 333 ms each, were taken at a voxel size of 32 μm. The resulting tiff stacks were processed with VG Studio Max (ver. 3.1; Volume Graphics, Charlotte, NC), Amira (version 6; FEI Visualization Science Group, Hillsboro, Oregon) and Meshlab (Cignoni et al., 2008).

Descriptive terminology for leaves follows that of the Manual of Leaf Architecture (Ellis et al., 2009); that for flowers and fruits follows Judd et al. (2016). Using the method proposed by Royer et al. (2007), the equation a+b*LOG(PW^2/A), where a is 3.070, b is 0.382, PW is petiole width, and A is leaf area, was used to estimate leaf dry mass per area (M_A). Measurements of the petiole and leaf area were obtained from the digital images using ImageJ and inputted to calculate an estimation of the M_A. Leaf mass per area is a proxy for leaf thickness; thicker leaves tend to be evergreen while thinner leaves are typically deciduous. The obtained values for species with multiple representative samples were averaged for inclusion in the equation. For the leaf of *Trochodendroides genetrix* (Newberry) Manchester, no complete leaf with the petiole attached was collected so an estimation of the total leaf area was made through comparison with complete leaves of that species from other sites. A threshold of 129 g/m^2 M_A (Royer et al., 2010), was used to differentiate deciduous and evergreen specimens, anything below a value of 129 g/m^2 M_A being deciduous and those with a higher value being determined as evergreen.

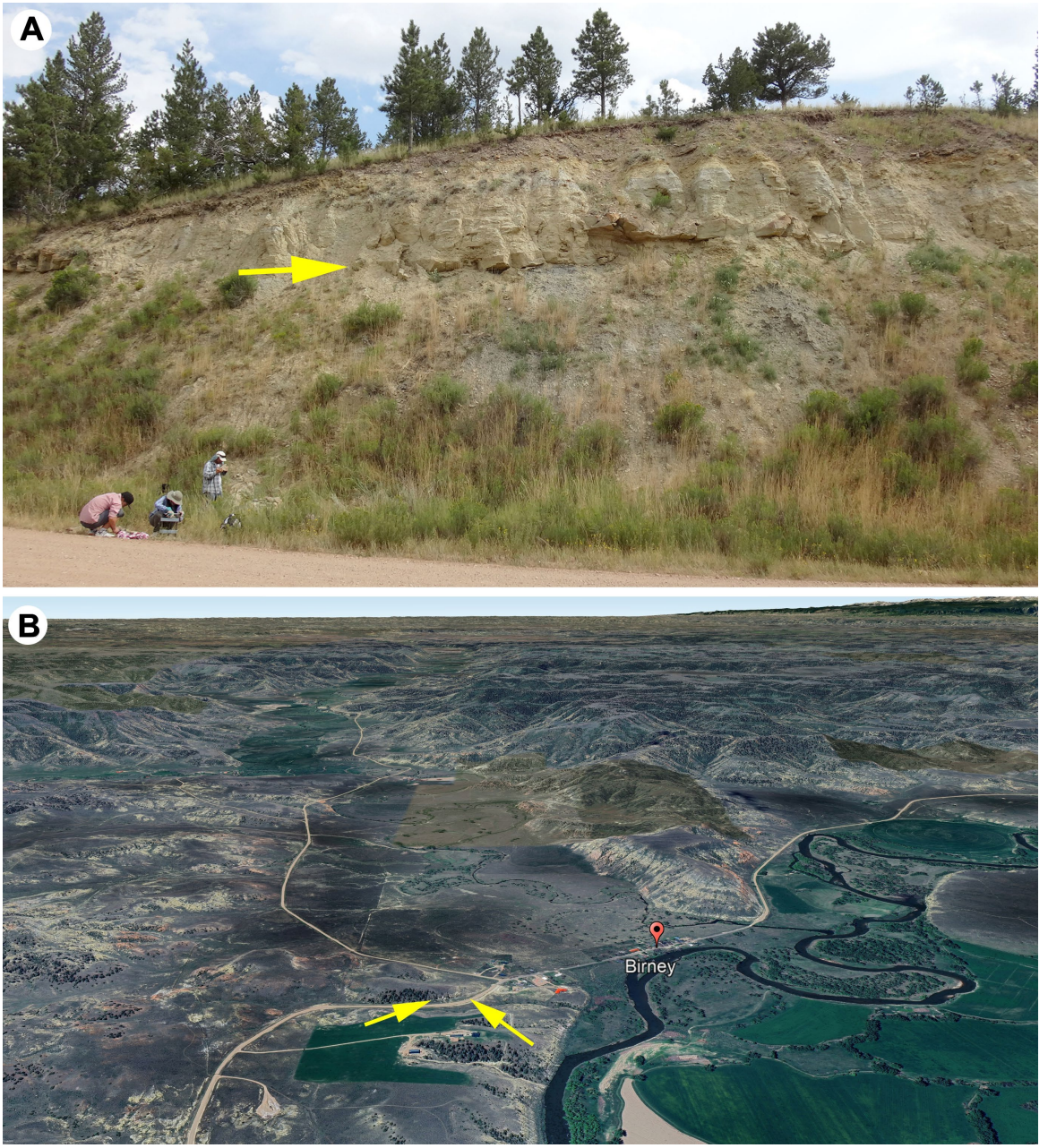

Figure 2. **A**. Birney outcrop at roadside, with arrow indicating where megafossils were collected. Photo credit: Jianhua Jin; **B**. Oblique aerial view with Birney locality in the foreground (arrows) looking south

RESULTS

SYSTEMATICS

We organized the information in this section starting with ferns, followed by angiosperms in the system of APGIV (2016) for those which we have confidence in their modern familial assignment, followed by those of uncertain systematic position, including the new genera and species.

Class POLYPODIOPSIDA
Cronquist, Takhtajan et Zimmerman 1966

Family indet.

Genus ***Dennstaedtia*** Bernhardi 1800

cf. ***Dennstaedtia americana***
Knowlton 1910

Fig. 3A–D

A single type of fern frond was recovered from the Birney site. It conforms in leaf form to that known elsewhere in the Paleocene

of North America as *D. americana* Knowlton (Brown, 1962; Manchester et al., 2023). Although no fertile fronds have been found at Birney or Horse Creek, the decurrence of pinnules on the rachis and venation, which may dichotomize up to three or four times within each pinnule, matches well with that seen in the fossils previously illustrated of this species. The original description of this species by Knowlton (1910) included a fertile frond, as well as sterile examples similar to those figured here. It is possible that this is a synonym of *D. blomstrandii* (Heer) Hollick (alternatively treated as *Coniopteris blomstrandii* (Heer) Kvacek et Manum) from the Paleocene of Alberta (G. Hoffman pers.comm., 2023).

Specimens examined. UF 18968-38355, 38356, 55390.

ANGIOSPERMS

Order PROTEALES
Jussieu ex Berchtold et J. Presl 1820

Family PLATANACEAE Lestiboudois 1826

Genus ***Platanus*** Linnaeus 1753

cf. ***Platanus***

Fig. 4E

Discussion. A single fruitlet ~10.8 mm long and 2.7 mm wide, with a narrowly obovate body and elongate style (4.4 mm long) is consistent in morphology with *Platanus*. The basal tuft of hairs characteristic of extant *Platanus* fruitlets is not seen in this specimen. Whether the hairs were originally absent (as in many Cretaceous and some early Cenozoic Platanaceae),

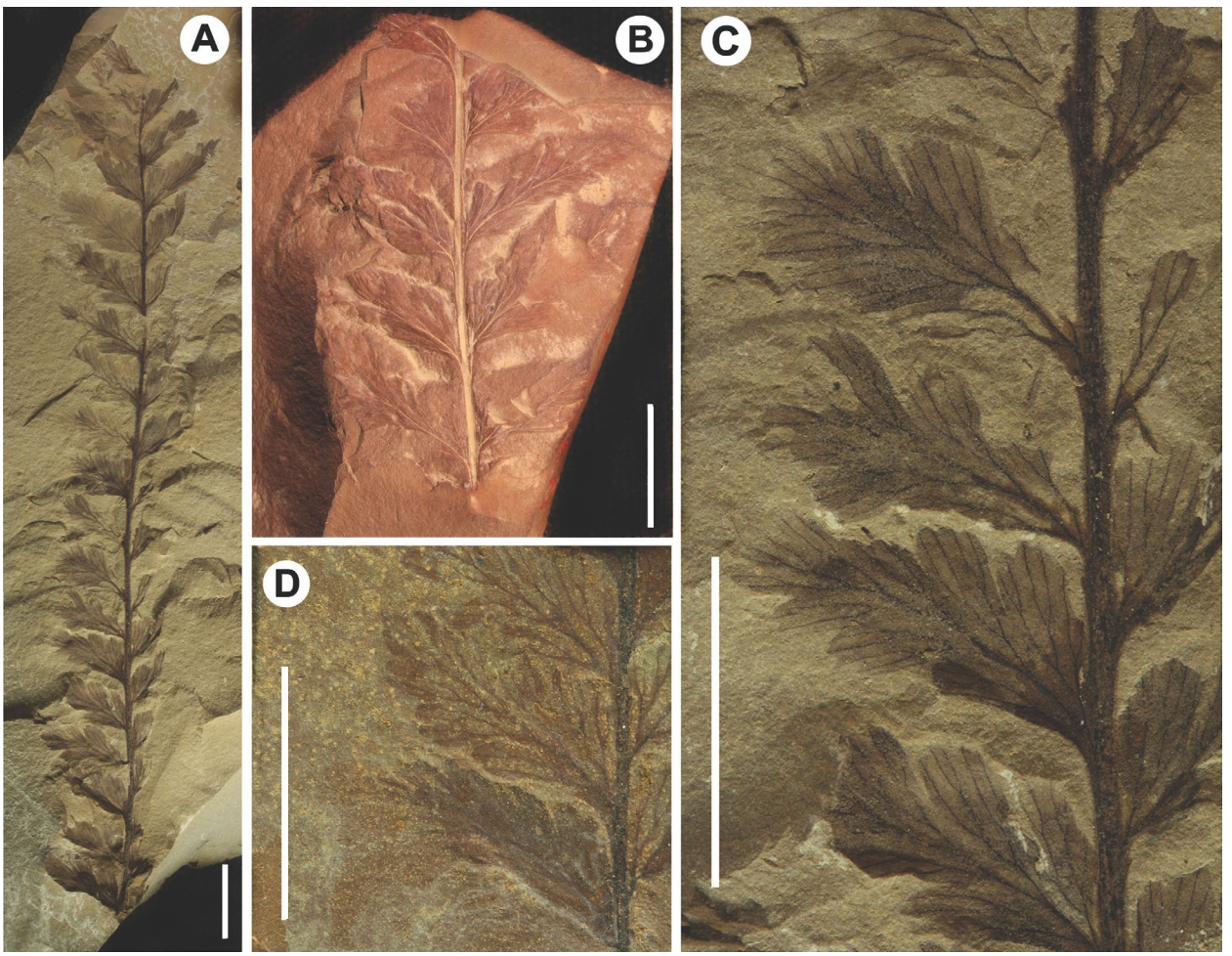

Figure 3. *Dennstaedtia americana* Knowlton. **A**. Elongate frond showing at least 20 pinnules on each side of the rachis, UF 18968-55390; **B**. Additional specimen showing several pinnae with distinct venation, UF 18968-38356; **C**. Enlargement of A showing details of three or more successive dichotomizing veins; **D**. Showing details of the dichotomizing venation within the pinnule, UF 18968-38355. Scale bars = 1 cm

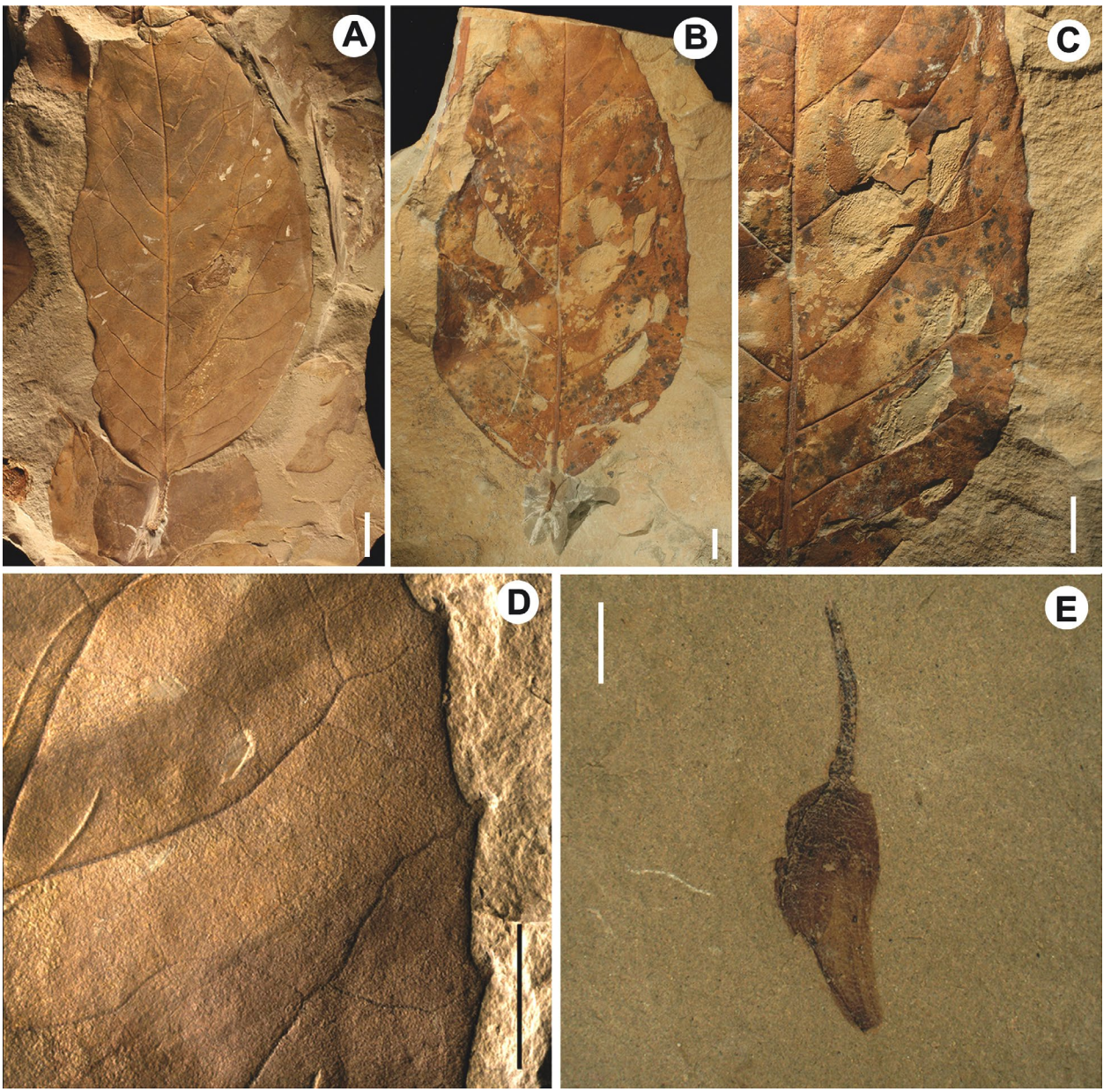

Figure 4. *Dyrana flexuosa* (Newberry) Golovneva. **A**. Typical leaf with narrow petiole and elliptical lamina with secondaries that are irregular in course with agrophic branches to the margin, UF 18968-50933; **B**. Leaf with elliptical and somewhat asymmetrical lamina, UF 18968-85267; **C**. Enlargement of B showing a serrate margin with widely spaced teeth; **D**. Enlargement of A showing rounded sinuses to the teeth and craspedodromous secondary veins, percurrent tertiary veins; **E**. Isolated platanus fruitlet, UF 18968-60416. Scale bars = 1 cm in A–C, 5 mm in D, 2 mm in E

or simply lost due to abrasion and/or deterioration prior to deposition is uncertain.

Specimen examined. UF 18968-60416.

Genus ***Dyrana*** Golovneva 1994

Dyrana flexuosa
(Newberry) Golovneva 2006

Fig. 4A–D

Description. Leaf simple, petiole length 1.1–1.2 cm. Lamina elliptic and somewhat asymmetrical, 150–110 mm long, 57–85 mm wide. Leaf unlobed, serrate over most of margin except lower 20% which is entire. Apex acute, base obtuse, convex. Ten secondary vein pairs, semicraspedodromous. Secondary veins arising decurrently, spacing gradually increases proximally. Secondary angle smoothly decreasing proximally. Agrophic veins common in lower half of lamina. Intersecondary veins absent. Teeth widely spaced, principal vein entering medially. Teeth rounded, apparently with glandular apices; sinuses rounded.

Discussion. Although common at some Paleocene sites (Brown, 1962, named as *Quercus*

sully Newberry), there are only a few specimens of this leaf type at Birney. It is recognizable by its moderately long petiole, pinnate semicraspedodromous venation, and margin that is entire near the base of the lamina but regularly toothed, with glandular teeth, over the upper ¾ of the lamina.

Specimens examined. UF 18968-50933, 85267.

Order TROCHODENDRALES
Takhtajan ex Cronquist 1981

Family cf. TROCHODENDRACEAE
Eichler 1865

Genus ***Zizyphoides*** Seward et Conway 1935

Zizyphoides flabella
(Newberry) Crane, Manchester et Dilcher 1991

Fig. 5A–F

Description. Leaves simple, petiole slender (0.4–0.7 mm thick), long (7–30 mm, commonly as long as the lamina). Lamina 40–60 mm long, 25–30 mm wide, ovate, elliptical, narrow or wide, varying from medially symmetrical to asymmetrical. Margin entire to crenate in the upper portion. Base symmetrical to asymmetrical, acute to obtuse, decurrent, concave and concavo-convex. Apex obtuse and rounded, sometimes retuse. Primary venation basal actinodromous. Secondary and tertiary veins brochidodromous. Higher order venation reticulate.

Discussion. This leaf type is common in Paleocene floras of North America, Greenland and Asia, and is commonly found together with *Nordenskioeldia* Heer fruits (Crane et al., 1991; Zolina et al., 2021).

Specimens examined. UF 18968-39037, 49667, 52146, 53388, 60414.

Genus ***Nordenskioeldia***
Heer 1870

Nordenskioeldia borealis Heer emend.
Crane, Manchester et Dilcher 1991

Fig. 6A–D

Discussion. Infructescence axes, fruitlets and elliptical winged seeds of *Nordenskioeldia* are present in the Birney collections. *Nordenskioeldia* fruits and *Zizyphoides* leaves are surmised to represent a single extinct plant taxon because the organs are found in co-occurrence at many Paleocene sites throughout the northern hemisphere (e.g. Crane et al., 1991; Manchester et al., 2023), and are even found together some Miocene sites (Manchester et al., 1991).

Specimens examined. UF 18968-39044, 53379.

Order SAXIFRAGALES
Berchtold et J. Presl 1820

Family CERCIDIPHYLLACEAE
Engler 1907

Genus ***Trochodendroides***
Berry 1922

Trochodendroides genetrix
(Newberry) Manchester 2014 leaf

Fig. 7A–G

Description. Leaves simple, petiole relatively long (14 mm). Lamina ovate, 74–100 mm long, 52–62 mm wide, margin serrate, rounded to cordate base, acute apex, straight margin. Venation pinnate; midvein prominent, two prominent ascending secondary veins arising from base; number of basal veins five. Secondaries festooned semicraspedodromous; angle of secondaries narrow at base, broadening towards the apex, about five pairs. Tertiaries irregularly reticulate, quaternaries somewhat irregular reticulate, areoles well developed, higher order venation obscured. Tooth spacing uniform, tooth distance regular. Absolute tooth spacing varies between specimens, although within each specimen it is uniform. Sinuses angular. Proximal flank straight to convex, distal flank straight to convex. Darkened glands present at the tip of each tooth, the principal vein enters medially and terminates into the gland.

Discussion. The serration in these leaves varies from fine to coarse (Fig. 7A–G), giving the appearance of more than one species. However, a specimen from the Paleocene of Killpecker Creek, Wyoming (Fig. 7.1 in Manchester, 2014) shows leaves of similar variation attached to a single twig. The radiation of the veins from the base of the lamina gives

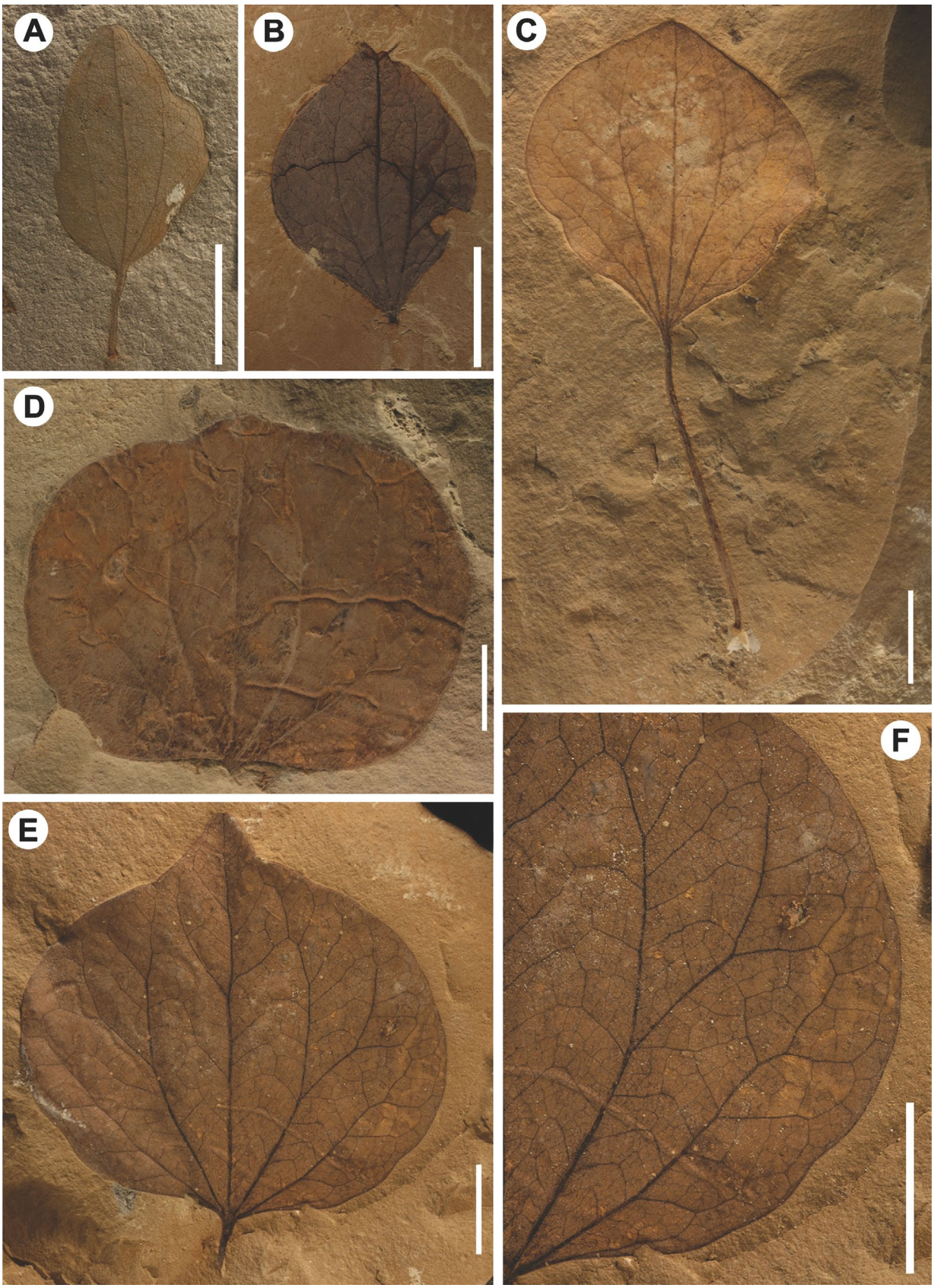

Figure 5. *Zizyphoides flabella* (Newberry) Crane, Manchester et Dilcher. **A**. Shows an irregularly crenate margin and a complete petiole slightly less than half the length of the lamina, UF 18968-53388; **B**. Shows pair of weaker secondary veins on either side of the midvein, with agrophic veins departing from the lateral primaries, UF 18968-60414; **C**. Complete leaf with petiole exceeding length of the lamina, showing the wide elliptical shape of the lamina and actinodromous venation, UF 18968-49667; **D**. Wide ovate lamina with actinodromous venation and blunt obtuse apex, UF 18968-39037; **E**. Wide ovate lamina with well-preserved actinodromous venation, UF 18968-52146; **F**. Enlargement of E to show higher-order venation and entire margin with no teeth. Scale bars = 1 cm

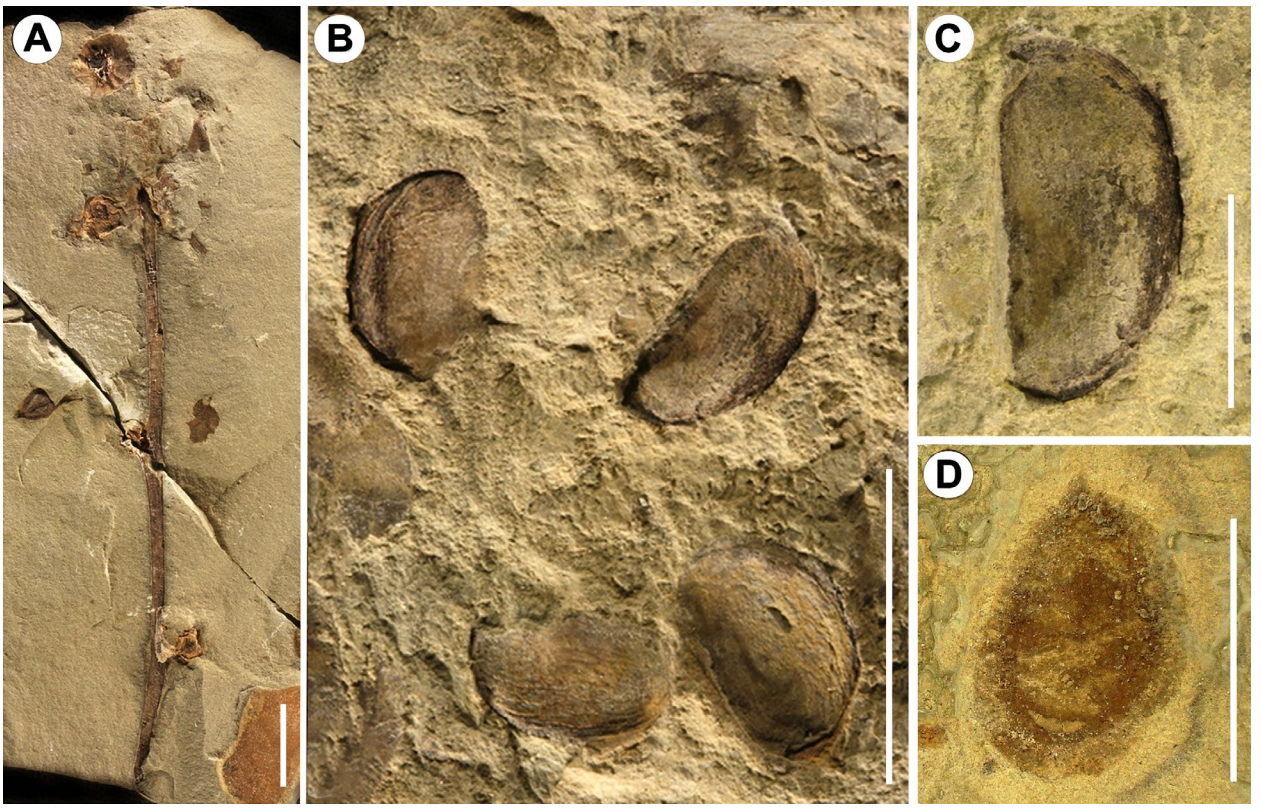

Figure 6. *Nordenskioeldia borealis* Heer. **A**. Infructescence that has shed most of its fruitlets, UF 18968-53379; **B–D**. UF 18968-39044; **B**. Isolated fruitlets; **C**. An isolated fruitlet showing flat ventral side and curved dorsal side, as well as striations; **D**. Isolated elliptical winged seed. Scale bars = 1 cm in A, B; 5 mm in C, D

an actinodromous appearance because the strongly ascending thick lateral secondaries resemble primary veins. The leaves of *Trochodendroides* are frequently found in association with pod-like fruits of *Jenkinsella* Reid et Chandler, and small winged seeds like those in Fig. 7F, G.

Specimens examined. UF 18968-38351, 50904, 50927, 50928, 50947.

Order FAGALES
Engler 1892

Family BETULACEAE
Gray 1821

Genus ***Corylites***
Gardner ex Seward et Holtum 1924

***Corylites* sp.**

Fig. 8A–C

Description. Leaf simple, lamina ovate, 35–63 mm wide, 59–95 mm long (n = 2); petiole length 20 mm, width 1.2 mm (n = 1). Lamina apex acute, straight, base cordate. Compound agrophic veins present. Major and minor secondaries craspedodromous. Intersecondaries apparently absent. Tertiaries prominently percurrent, straight near the apex, and convex-rounded to sinuous near the base. Quarternaries alternate percurrent. Margin serrate with weakly compound teeth, somewhat larger teeth at agrophic secondary vein termination and smaller teeth intervening. Teeth acute, straight proximally and distally, sharp to sometimes rounded, non-glandular, and very angular sinuses. Principal vein enters medially to the tooth apex, accessory veins branch off to join the adjacent sinuses.

Discussion. Leaves of this genus are rare at Birney, found in a somewhat coarser siltstone than most of the other fossils. They resemble those of extant *Corylus* L., but also conform to the type of leaf commonly associated with fruits of the extinct genus *Palaeocarpinus* Crane (Manchester and Chen, 1996; Manchester et al., 2004; Correa-Narvaez and Manchester, 2021); however, we did not find any fruits of *Palaeocarpinus* at this site.

Specimens examined. UF 18968-49696, 56260.

Order SAPINDALES
Jussieu ex Berchtold et J. Presl 1820

Family SAPINDACEAE Jussieu 1789

Genus ***Aesculus*** Linnaeus 1753

Aesculus hickeyi Manchester 2001

Fig. 9A–D

Description. Leaves palmately compound, commonly with three leaflets, sometimes with five. Leaflets obovate, 5–9 cm long, 2–5 cm wide, acute bases and apex. Petiole 2.3 cm long, 0.12 cm wide. Middle leaflet longer than outer leaflets. Margin finely serrate with closely spaced, non-glandular teeth and angular sinuses. Secondaries craspedodromous. Intersecondaries rare. Tertiaries straight, weakly impressed, oppositely percurrent.

Discussion. Complete palmately compound leaves, commonly with three leaflets, sometimes with five, are common at the Birney site. Although fruit capsules and seeds of *Aesculus* are known from other sites in the Paleocene of Wyoming and North Dakota (Manchester, 2001) we did not find verifiable reproductive remains of this kind in the Birney deposit.

Specimens examined. UF 18968-50961, 52144, 85252.

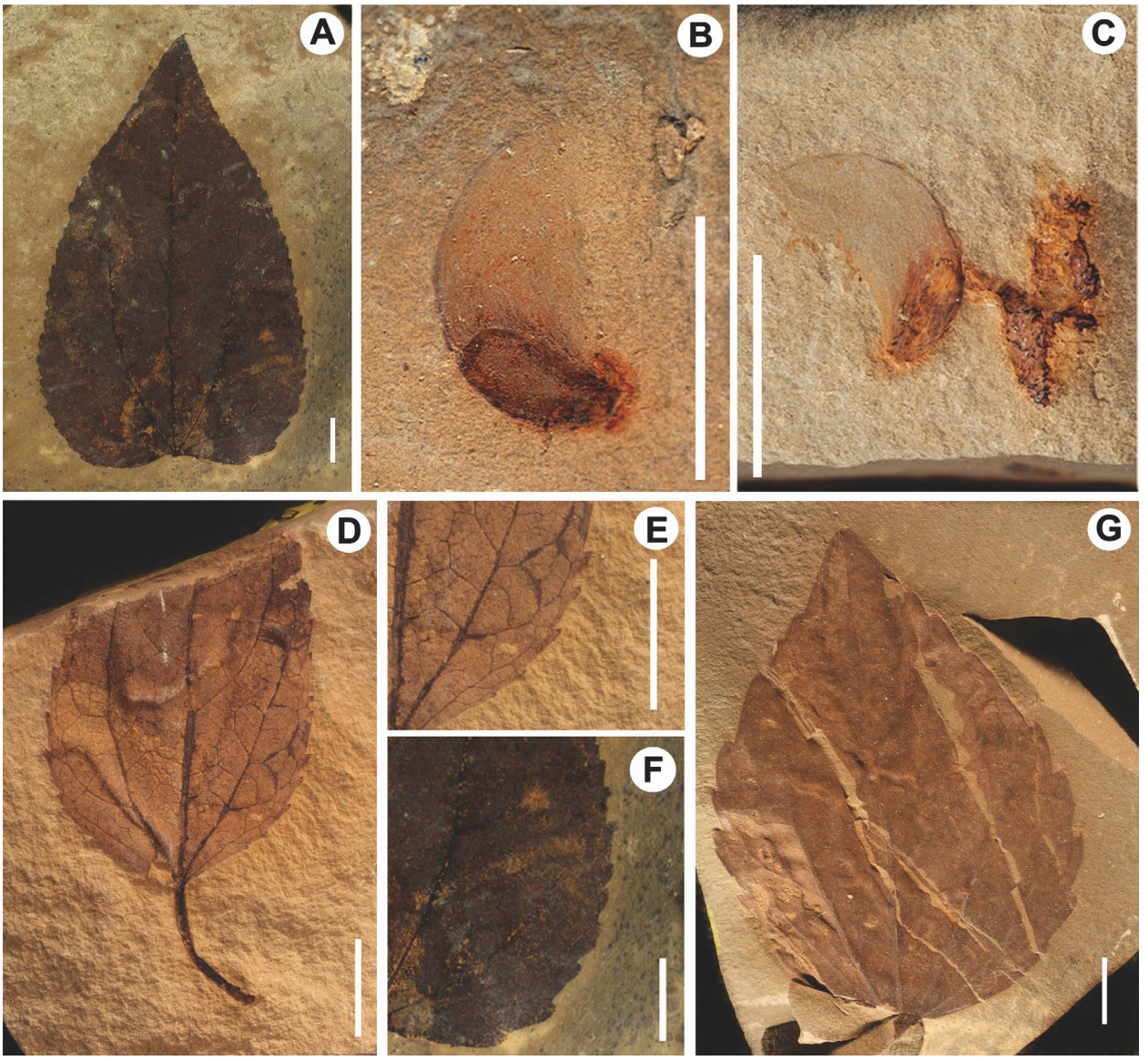

Figure 7. *Trochodendroides genetrix* (Newberry) Manchester. **A**. Lamina with a finely serrate margin, cordate base and acute apex, UF 18968-50947; **B**, **C**. Winged seeds of probable affinity with *Trochodendroides*, UF 18968-38351, 50928; **D**. Elliptical lamina with long petiole, prominently serrate margin, UF 18968-50927; **E**. Enlargement of D showing fine venation adjacent to teeth; **F**. Enlargement of margin of A with blunt teeth and sharp sinuses; **G**. Ovate leaf with actinodromous venation and rounded base acute apex, UF 18968-50904. Scale bars = 1 cm in A, C–F; 5 mm in B

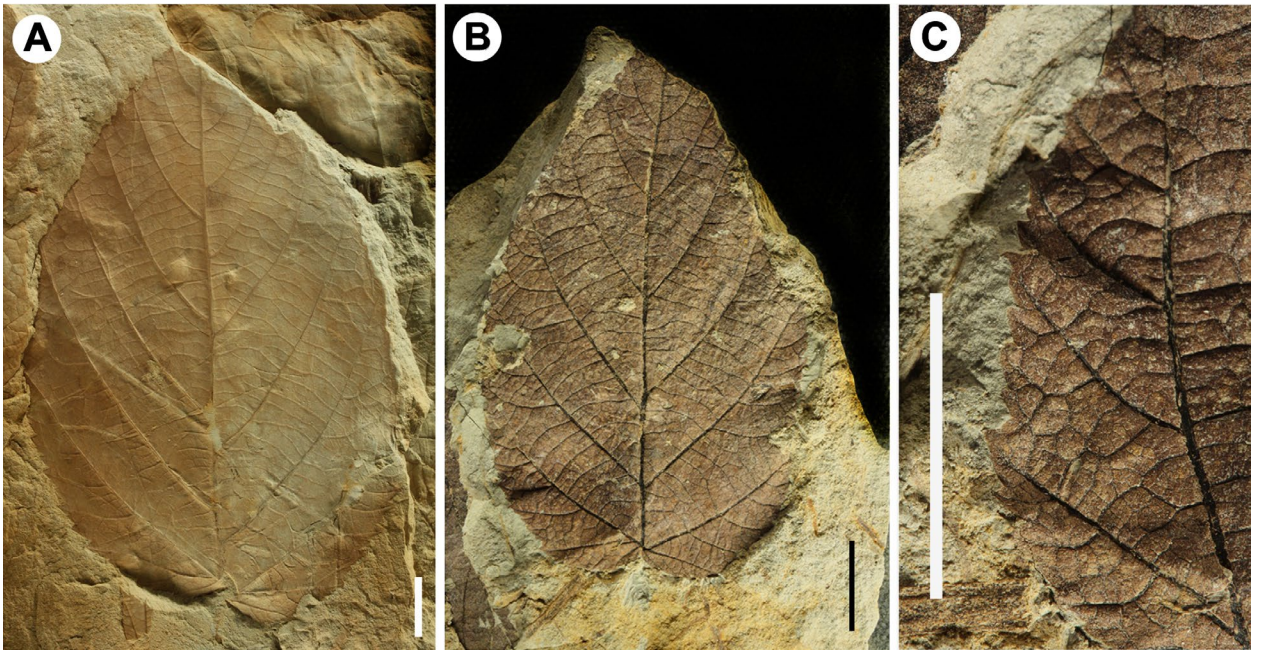

Figure 8. *Corylites* sp. **A**. Ovate leaf with cordate base showing craspedodromous secondaries and strongly percurrent tertiaries, UF 18968-49696; **B**. Leaf showing compound agrophic veins present and acute teeth with angular sinuses, UF 18968-56260; **C**. Enlargement of B, showing principal vein entering tooth medially, and accessory veins that branch to the sinuses. Scale bars = 1 cm

Order CORNALES Link 1829

Family NYSSACEAE
Jussieu ex Dumortier 1829

Genus ***Davidia*** Baillon 1871

Davidia antiqua
(Newberry) Manchester 2002

Fig. 10A–F

Description. Leaves simple, petiole 0.1–0.2 cm wide, 2–5 cm long. Lamina moderate to widely ovate, base obtuse, cordate; apex obtuse, convex to rounded. Margin serrate with regularly spaced, blunt, non-glandular teeth, sinuses subrounded or angular. Primary vein monopodial. Secondary veins pinnate, craspedodromous, eight pairs. Intersecondaries absent. Compound agrophic veins present. Tertiary veins well impressed, opposite percurrent, straight. Fourth and fifth order veins reticulate.

Discussion. *Davidia antiqua* is represented both by leaves (Fig. 10A–D) and fruits (Fig. 10E, F) in the Birney florule. The leaves are recognizable by the combination of strictly craspedodromous secondary and agrophic veins, simple teeth, percurrent tertiary veins, commonly cordate base, and long petioles. The ellipsoidal fruits with prominent longitudinal ribs correspond to those known more completely from permineralized specimens matching the internal morphology and anatomy of extant *Davida* (Manchester, 2002). This species was widespread in the Paleocene of western North America although the genus is now native only to China (Manchester, 2002; Manchester et al., 2023). Other genera of Cornales which are common elsewhere in the Fort Union Formation, such as *Cornus* (Manchester et al., 2009) and *Beringiaphyllum* Manchester, Crane et Golovneva (Manchester et al., 1999), have not been recovered from the Birney florule.

Specimens examined. UF 18968-38340, 38343, 49697, 50923A, 50925.

Genus ***Browniea***
Manchester et Hickey 2007

Browniea serrata
(Newberry) Manchester et Hickey 2007

Fig. 11A–E

Discussion. A few specimens from the Birney site conform in leaf architecture with the extinct genus *Browniea*, which is related to the extant Chinese genus *Camptotheca* Decne. Although infructescences and dispersed fruits of *Browniea* are common at many other North American

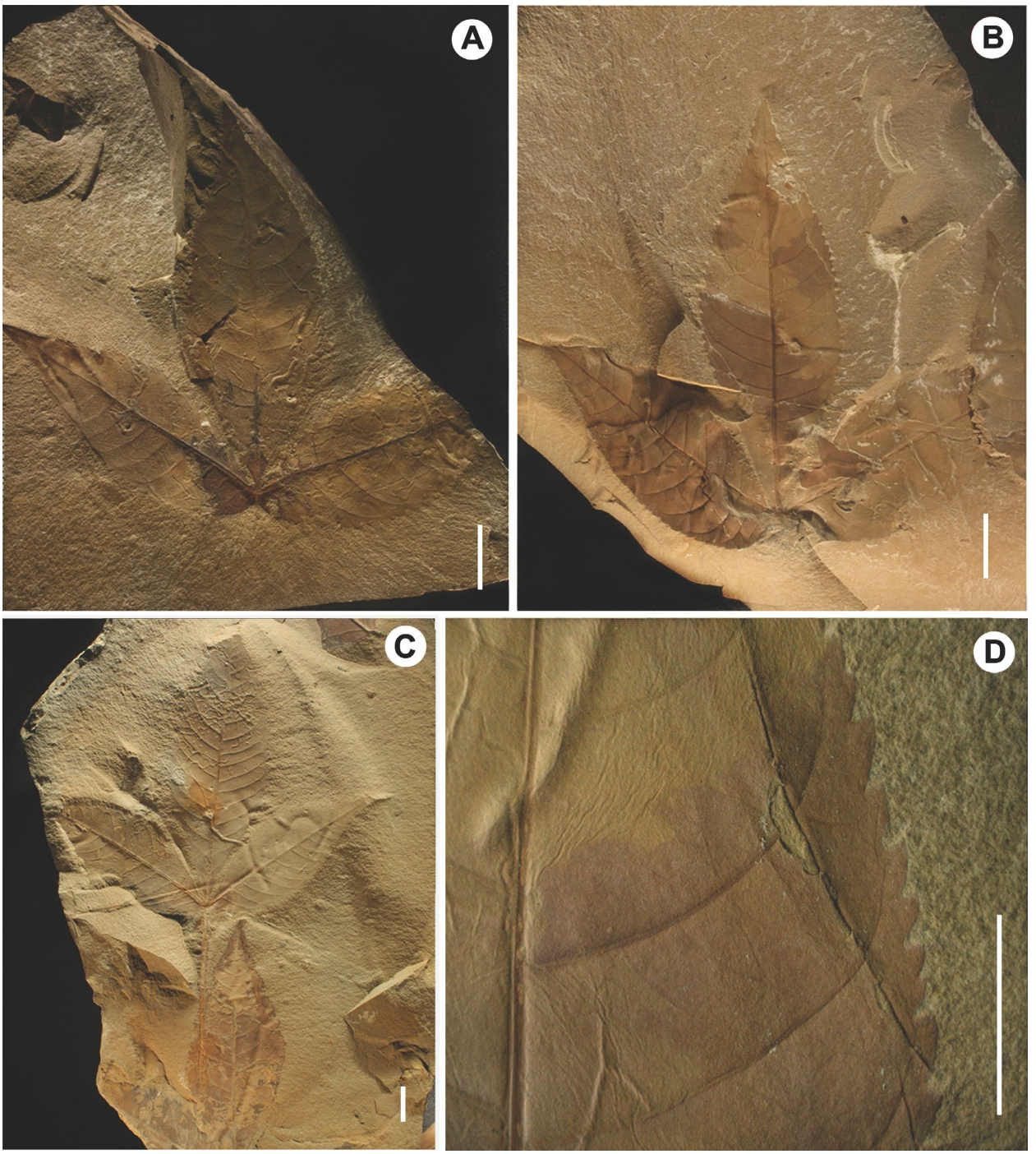

Figure 9. *Aesculus hickeyi* Manchester. **A**. Typical leaf with three leaflets. Composite image prepared from individual photographs of each counterpart overlayed, UF 18968-50961; **B**. Compound leaf showing finely serrated margin, UF 18968-52144; **C**. Compound leaf showing long petiole and widely spaced secondary veins, UF 18968-85252; **D**. Enlargement of B showing angular sinus to the teeth, with sharp apices, non-glandular, with principal vein medial in some cases and others supramedial. Scale bars = 1 cm in A–C, 5 mm in D

Paleocene sites (Manchester and Hickey, 2007), including several nearby sites in the Tongue River Member in eastern Montana, we failed to find fruiting material at Birney. Leaves, measuring 56–76 mm in length and 45–59 mm in width, are recognized by their commonly cordate bases, pinnate secondary venation, lack of intersecondary veins, few or no agrophic veins, percurrent tertiary veins that are mostly opposite, and regularly spaced simple, apparently non-glandular teeth with the principal vein of each tooth entering medially. In some of these features they resemble the related genus *Davidia*, treated above, but the secondary veins of *Browniea* are semicraspedodromous, forming successive loops at the margin (Fig. 11A–E), in contrast to the straight craspedodromous secondaries of *Davidia* (Fig. 10A–D).

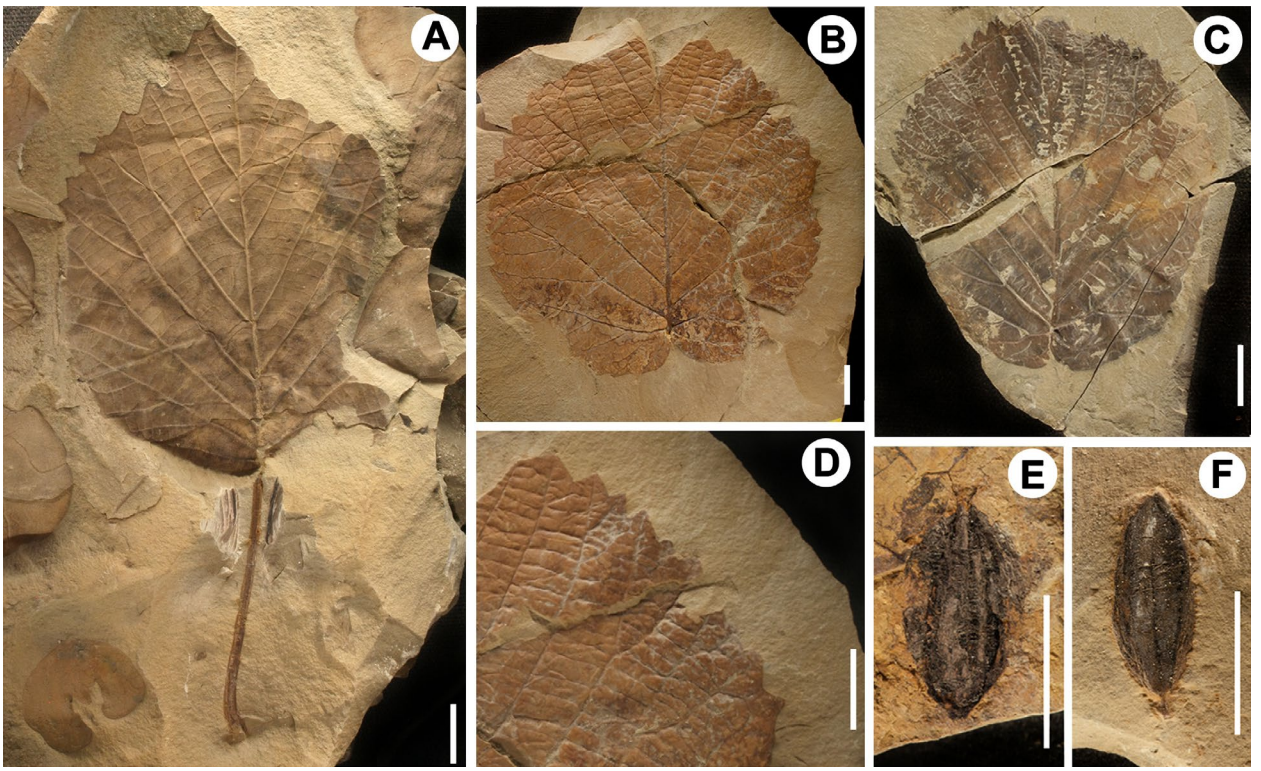

Figure 10. *Davidia antiqua* (Newberry) Manchester. **A**. Ovate lamina with long petiole, UF 18968-49697; **B**. Widely ovate lamina with cordate base, pinnate craspedodromous secondary veins, UF 18968-38343; **C**. Widely elliptical lamina with a blunt rounded apex, UF 18968-38340; **D**. Enlargement of B showing prominent and parallel percurrent tertiary veins and agrophic veins branching off the secondaries and blunt non-glandular teeth; **E**, **F**. Isolated endocarps showing elliptical outline and longitudinal grooves, UF 18968-50923A, 50925 respectively. Scale bars = 1 cm

Specimens examined. UF 18968-38342, 50935, 61839.

Order INDET

Genus ***Phyllites*** Brongniart 1822

Phyllites demoresii Brown 1962

Fig. 12A–I

Discussion. These leaves correspond to those known from other Paleocene North American sites as *Phyllites demoresii* Brown (1962). Distinctive features include long petioles of 10–20 mm in length and 1.1–1.2 mm in width, and moderately large, entire-margined laminae up to 9 cm long and 6–7 cm wide, with widely spaced secondary veins of irregular course, forming conspicuous loops well within the margin, and common intersecondary veins. Co-occurrence of such leaves with the fossil fruits of *Porosia* Hickey (see below) provides circumstantial evidence that they may represent the same extinct plant species (Manchester et al., 2023). Specimen UF 18968-55580 (Fig. 12H) differs from the other specimen figured here, with secondaries of straighter course and wider angles basally, and could represent either intraspecific variation or perhaps the leaf of another taxon.

Specimens examined. UF 18968-38363, 49698, 55579, 55580, 60424, 60425, 61842, 66422.

Genus ***Porosia*** Hickey 1977

Porosia verrucosa (Lesquereux) Hickey emend. Manchester et Kodrul 2014

Fig. 13A–F

Discussion. Fruits of *Porosia* are common, existing from the Late Cretaceous (Maastrichtian) to the early Eocene, and can be found throughout western North America and eastern Russia, indicating a distribution that spread across the Beringia land bridge. Several specimens from Birney have been figured previously in a more detailed treatment of the genus (Manchester and Kodrul, 2014). These fruits are reniform, ~2 cm long and 1.5 cm wide, with a prominently punctate surface and are commonly found with sediment-filled cylindrical tubercles, and borne on pedicels

singly or in pairs (Manchester and Kodrul, 2014). *Porosia* fruits frequently co-occur with the leaves of *Phyllites demoresii* mentioned above, and it is possible that they represent the same parent plant (Manchester et al., 2023).

Specimens examined. UF 18968-34511, 38354, 49681–49683, 50911–50920, 52149, 52150, 53384–53386, 60413.

Genus ***Arthayesia***
Wilder et Manchester **gen. nov.**

Etymology. This genus is named in honor of local ranchers Arthur Hayes Sr. and Arthur Hayes Jr., who encouraged our investigation of the fossils from the Birney region.

Plant Fossil Names Registry. PFN003509 (for generic name).

Generic diagnosis. Leaves petiolate, petiole short. Lamina elliptic, symmetrical, straight to semicraspedodromous venation, rounded convex base, straight to acuminate acute apex. Secondary veins semicraspedodromous. Intersecondaries present and common. Tertiary veins percurrent, varying from straight to sinuous, angle increasing proximally. Fourth and fifth order veins irregularly reticulate, quaternaries reticulate.

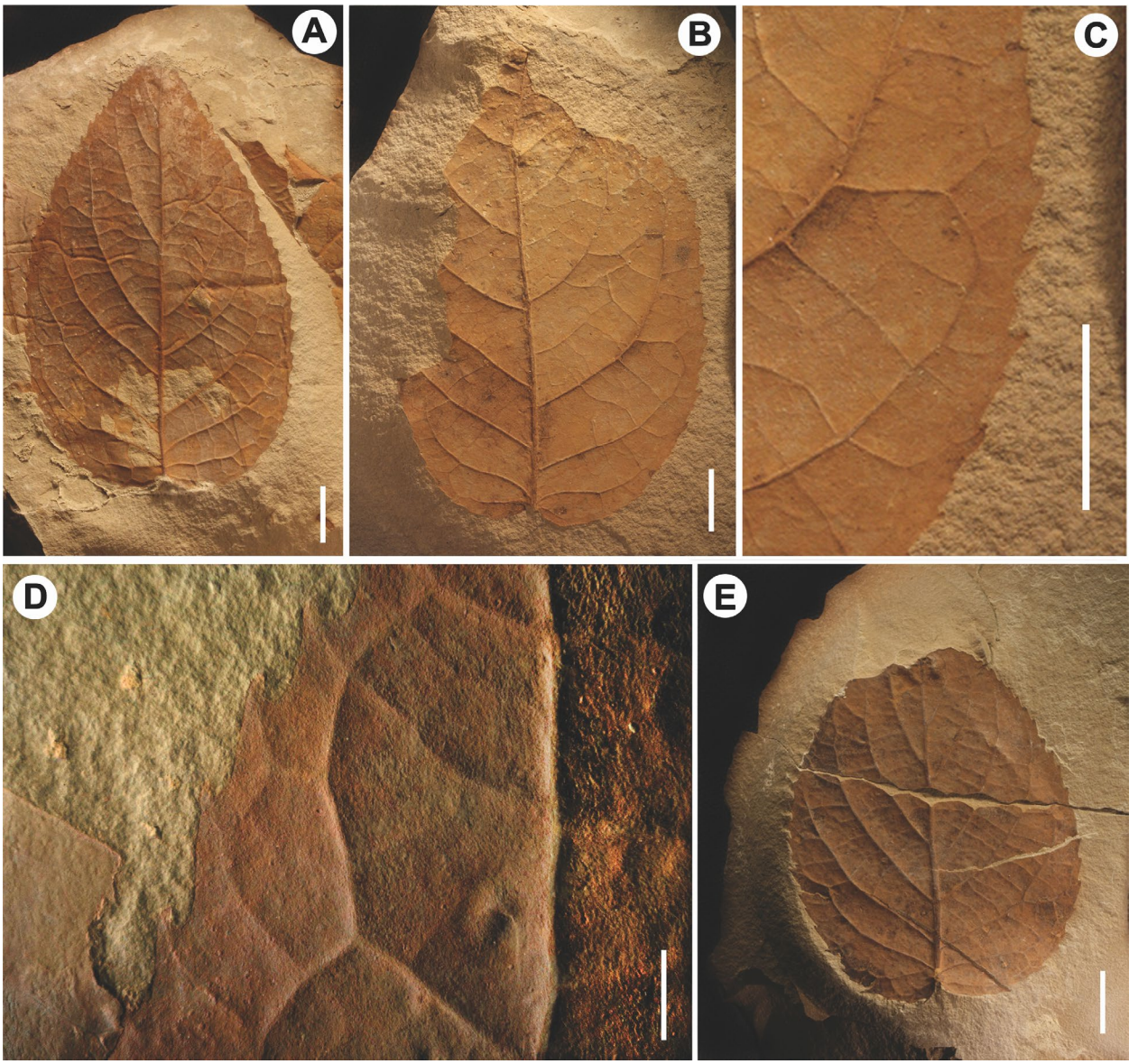

Figure 11. *Browniea serrata* (Newberry) Manchester et Hickey. **A**. Typical leaf with short petiole, acute apex, cordate base, and serrate margin, UF 18968-38342; **B**. Leaf showing cordate base, semicraspedodromous secondaries, and intersecondary veins present, UF 18968-50935; **C**. Enlargement of B showing non-glandular regularly spaced teeth; **D**. Enlargement of A, showing serrate margin with principal vein entering tooth medially; **E**. Leaf showing semicraspedodromous secondaries and craspedodromous near apex with percurrent tertiaries, UF 18968-61839. Scale bars = 1 cm in A–C, E; 2 mm in D

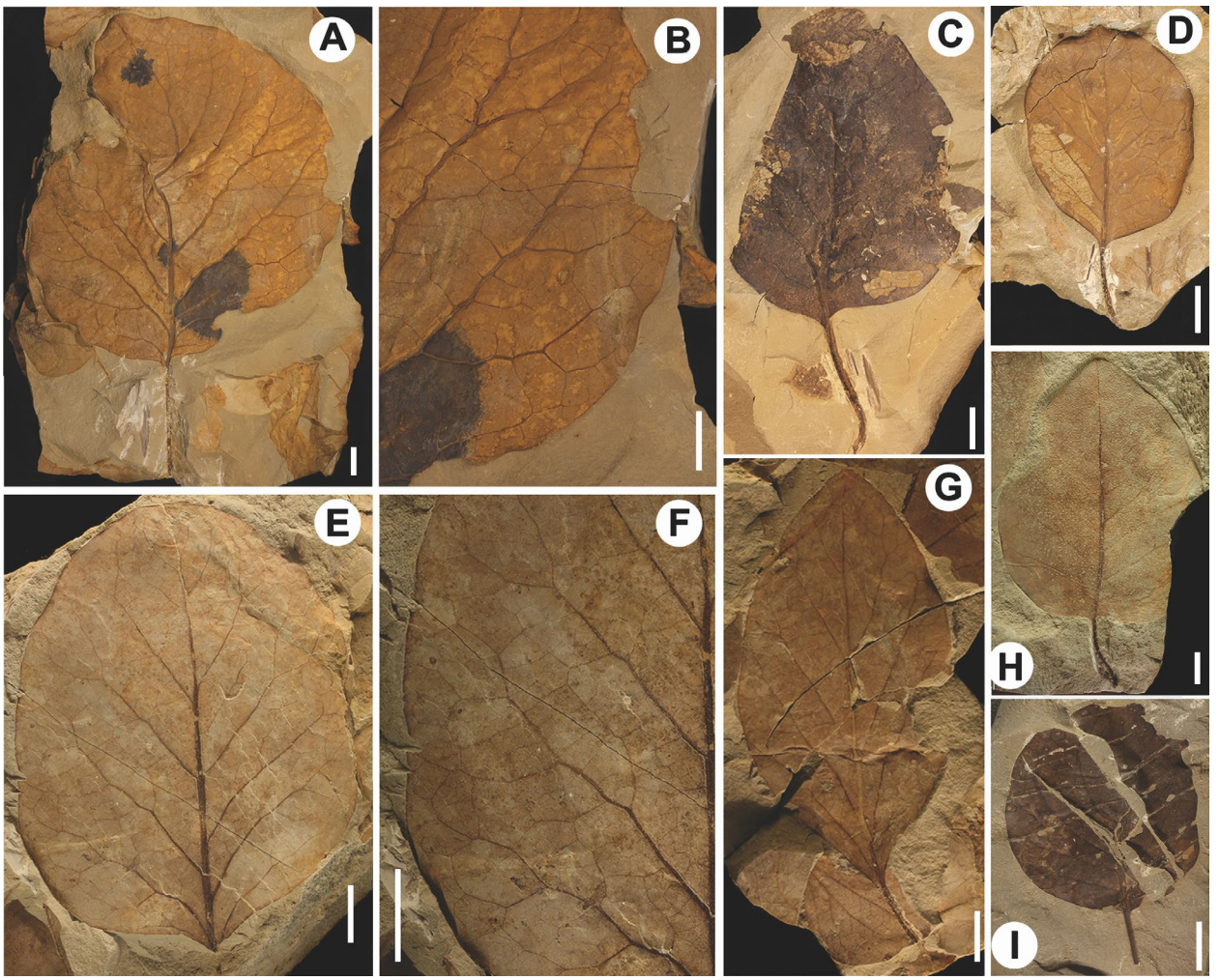

Figure 12. *Phyllites demorsesii* Brown. **A**. Typical leaf with a long petiole, ovular shaped lamina, UF 18968-60425; **B**. Enlargement of A showing secondaries of irregular course; **C**. Leaf with long petiole, UF 18968-49698; **D**. Leaf with decurrent base, UF 18968-38363. **E**. Wide, entire margin leaf showing a rounded apex, UF 18968-60424; **F**. Enlargement of E, showing secondaries of irregular course; **G**. Narrow leaf with long petiole, decurrent base, UF 18968-66422; **H**. Specimen with rounded apex, secondaries of a straighter course, and wide basal secondary angles, UF 18968-55580; **I**. UF 18968-61842. Scale bars = 1 cm

Teeth small, regularly spaced, with rounded sinuses and glandular apices. Teeth vary in degree of hookedness.

Type species. *Arthayesia brevipetiolata* Wilder et Manchester sp. nov.

Arthayesia brevipetiolata
Wilder et Manchester **sp**. **nov**.

Fig. 14A–I

Etymology. The epithet refers to the short petiole characteristic of this species.

Plant Fossil Names Registry. PFN003510 (for species name).

Specific diagnosis. Same as for genus.

Holotype here designated. UF 18968-50969.

Paratypes. UF 18968-50959, 61840, 50963, 50970, 60415.

Type locality. North side of Birney, Rosebud County, Montana, USA, 45°19.53384′N, 106°30.49632′W.

Description. Petiole short, (length 0.2–0.7 cm; width 0.1–0.2 cm. Lamina 5.5–21 cm long, 3–9 cm wide. Margin serrate with small regularly spaced teeth, with rounded sinuses, distal flank concave, proximal flank retroflexed, frequently giving a hook-like appearance. Principal vein terminates at the tooth apex where a dark dot suggests the presence of a gland (Fig. 14G, H).

Discussion. This is the most common leaf type at the Birney site, but we have not noticed it at other sites including those treated in Brown's monograph of the Paleocene flora of the Rocky Mountains and Great Plains region (Brown, 1962; Manchester, 2014), nor in other Paleocene floras such as those of North

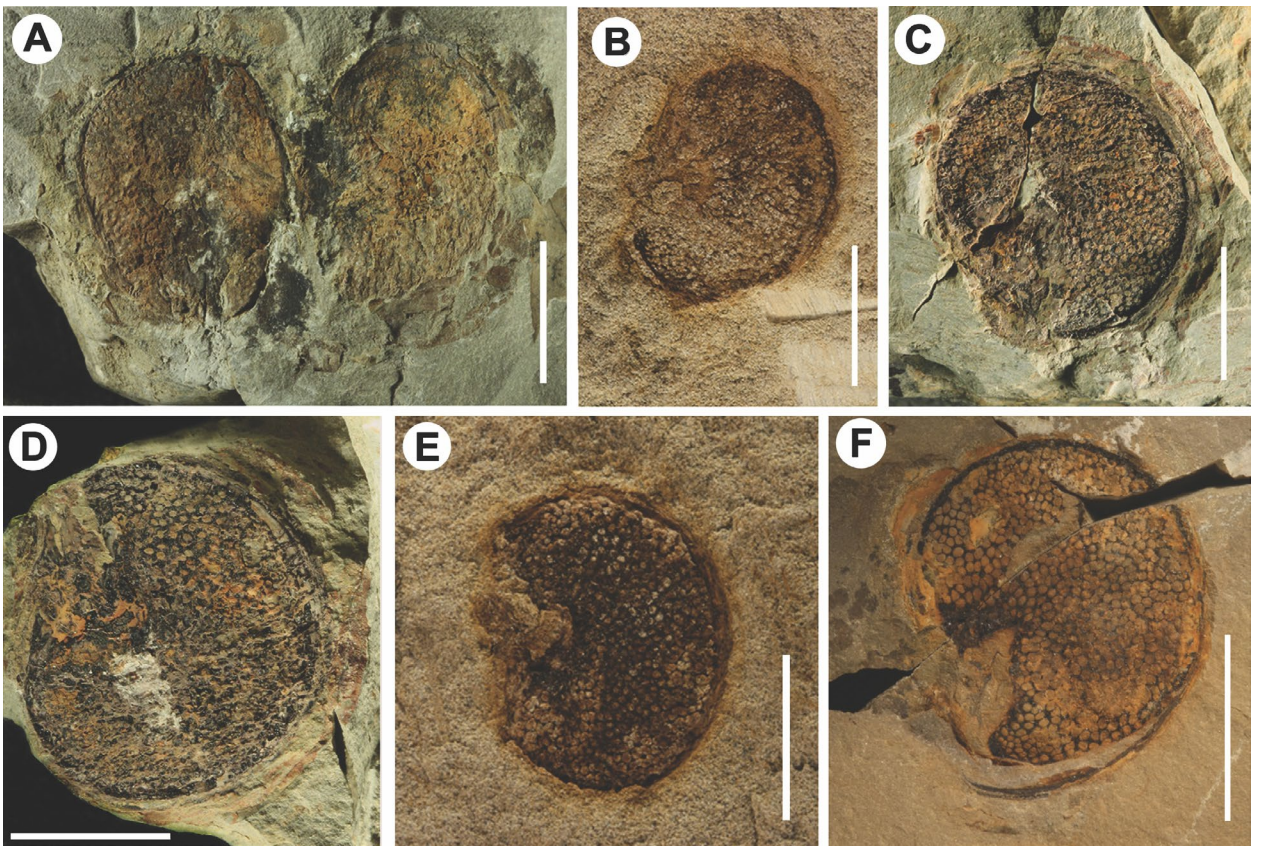

Figure 13. *Porosia verrucosa* (Lesqueruex) Hickey emend. Manchester et Kodrul. **A**. Pair of mericarps, UF 18968-050918; **B**. Isolated mericarp, UF 18968-50913'; **C**. UF 18968-050912; **D**. Counterpart of C, UF 18968-050912'; **E**. Isolated mericarp showing reniform shape, UF 18968-50913; **F**. UF 18968-50911. Scale bars = 1 cm

Dakota (Hickey, 1977), and Alberta (McIver and Basinger, 1993). It is distinguished by its short, thick petioles, small, evenly spaced, and sometimes hooked teeth, and elliptic lamina with rounded base, and acute apex, with semicraspedodromous secondary veins. Unlike *Dyrana* Golovneva which can have a similar general appearance, these leaves have serrations continuing to the very base of the lamina, and they lack agrophic veins. There is some variation in teeth, with leaves such as Fig. 14C that are very hook-like, with concave apical flanks, distinguishing them from the less hooked teeth seen on the holotype and other specimens.

Genus ***Birneyphyllum***
Wilder et Manchester **gen**. **nov**.

Etymology. The generic name denotes leaves with their type locality near the town of Birney, Montana.

Plant Fossil Names Registry. PFN003511 (for generic name).

Generic diagnosis. Leaf simple, petiolate. Lamina elliptical, prominently pinnately lobed, with a serrate margin. Base acute and decurrent, apex acute. Venation pinnate with regularly spaced secondary veins that reach from the midvein to the tips of each lobe. Intersecondary veins occasional. Intramarginal vein well inside margin. 3–4 or more pinnate tertiary veins per lobe. Sinuses between lobes sharp and acute. Each lobe has an intramarginal vein formed by successively looping tertiary veins. Tertiary veins pinnate within lobes. Lobes acute with somewhat rounded tips. Marginal teeth acute, evenly spaced with sharp sinuses. Principal vein entering the tooth supramedially.

Type species. *Birneyphyllum lobata* Wilder et Manchester sp. nov.

Birneyphyllum lobata
Wilder et Manchester **sp**. **nov**.

Fig. 15A–E

Etymology. The epithet lobata refers to the strongly lobed lamina in this species.

Plant Fossil Names Registry. PFN003512 (for species name).

Specific diagnosis. Same as for the genus.

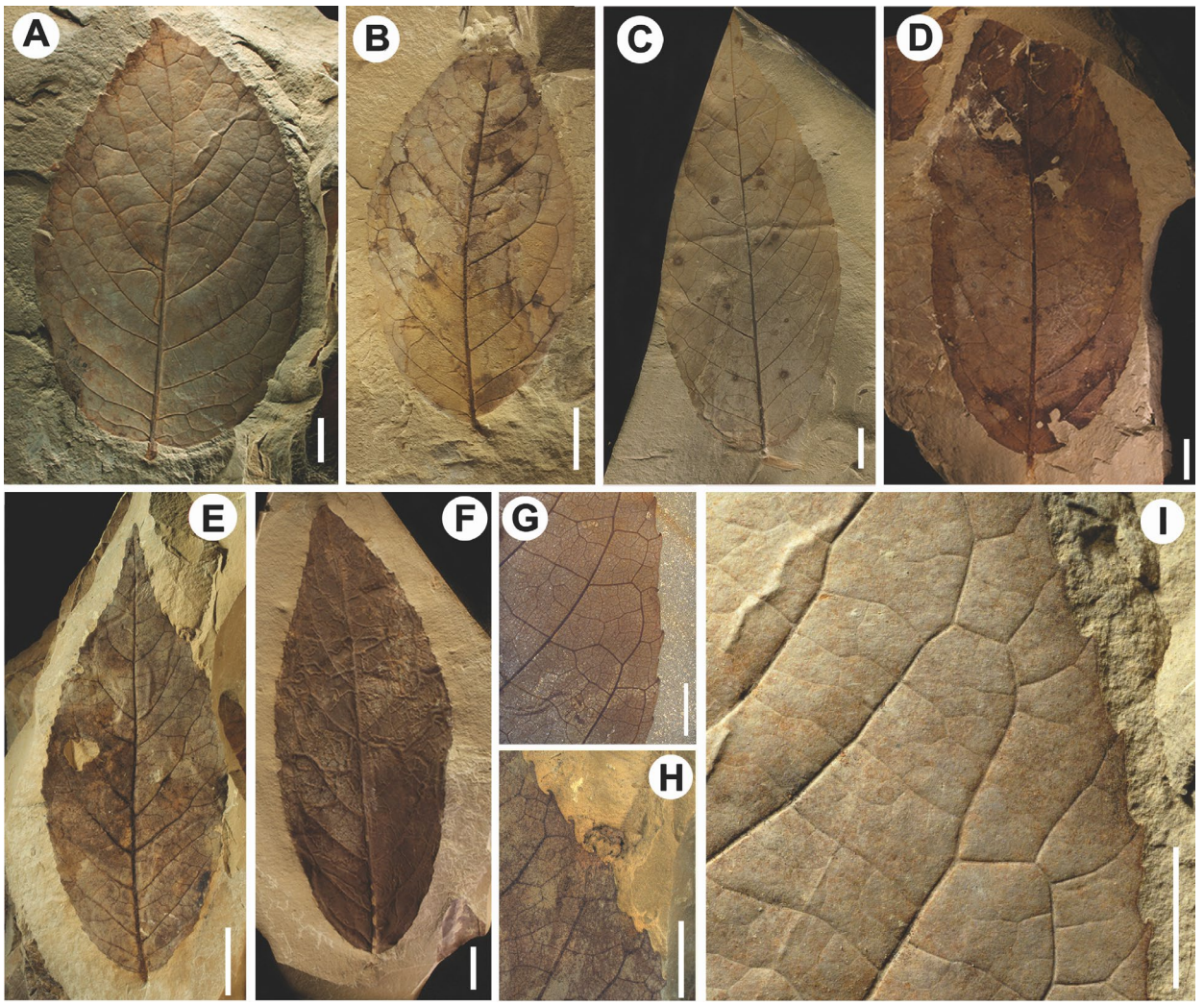

Figure 14. *Arthayesia brevipetiolata* gen. et sp. nov. **A**. Holotype, with typical short petiole, elliptical lamina, serrate margin, and semicraspedodromous venation, UF 18968-50969; **B**. Another typical leaf with semicraspedodromous venation, with obvious looping, short petiole, and finely serrated margins, UF 18968-50959; **C**. Leaf with very short petiole and elliptically shaped lamina, UF 18968-61840. **D**. Elliptical leaf with short petiole UF 18968-50970; **E**. Leaf with acuminate apex, UF 18968-50963; **F**. Narrow leaf with acute apex and finely serrated margins, UF 18968-60415; **G**. Enlargement of C showing percurrent tertiaries and a well-defined higher order reticulum, highly branched freely ending veinlets, and teeth with dark tips suggesting that they are glandular, and varying hook-like teeth with rounded to straight to convex sinuses, UF 18968-61840; **H**. Enlargement of D specimen with hook-like teeth, with varying prominences of hooks; **I**. Enlargement of A, showing small regularly spaced teeth with the principal vein terminating at the apex. Scale bars = 1 cm in A–D, F–I; 5 mm in E

Holotype here designated. UF 18968-61841.

Paratype. UF 18968-59694.

Type locality. North side of Birney, Rosebud County, Montana, USA, 45°19.53384′N, 106°30.49632′W.

Description. Petiole length 2.4–2.5 cm and width 0.18 cm, Lamina elliptical, prominently pinnately lobed (Fig. 15A, C, E) with a finely serrate margin (Fig. 15B, E). Lamina 11 cm long (n = 1) and 3–4, avg. 3.5 cm wide (n = 2), ~2.75 times longer than wide. Secondary veins arise at angles of 40° from midvein. Sinuses between lobes braced by a strong vein arising from a secondary vein beneath that sinus. The incision between lobes is about half the length from the tip to the midvein. Marginal teeth acute, evenly spaced with sharp sinuses. Principal vein entering the tooth supramedially. Both teeth and lobes have circular tan-colored glands at their tips (Fig. 15B).

Discussion. This pinnately lobed leaf type is represented by only two faintly preserved specimens and, to our knowledge, has not been found at other fossil sites. The pinnately organized tertiary veins within the lateral lobes are distinctive, as are the evenly spaced, small glandular teeth along the margins. The relationship with modern families remains to be determined. The leaf might have affinity to Rosaceae, as there are

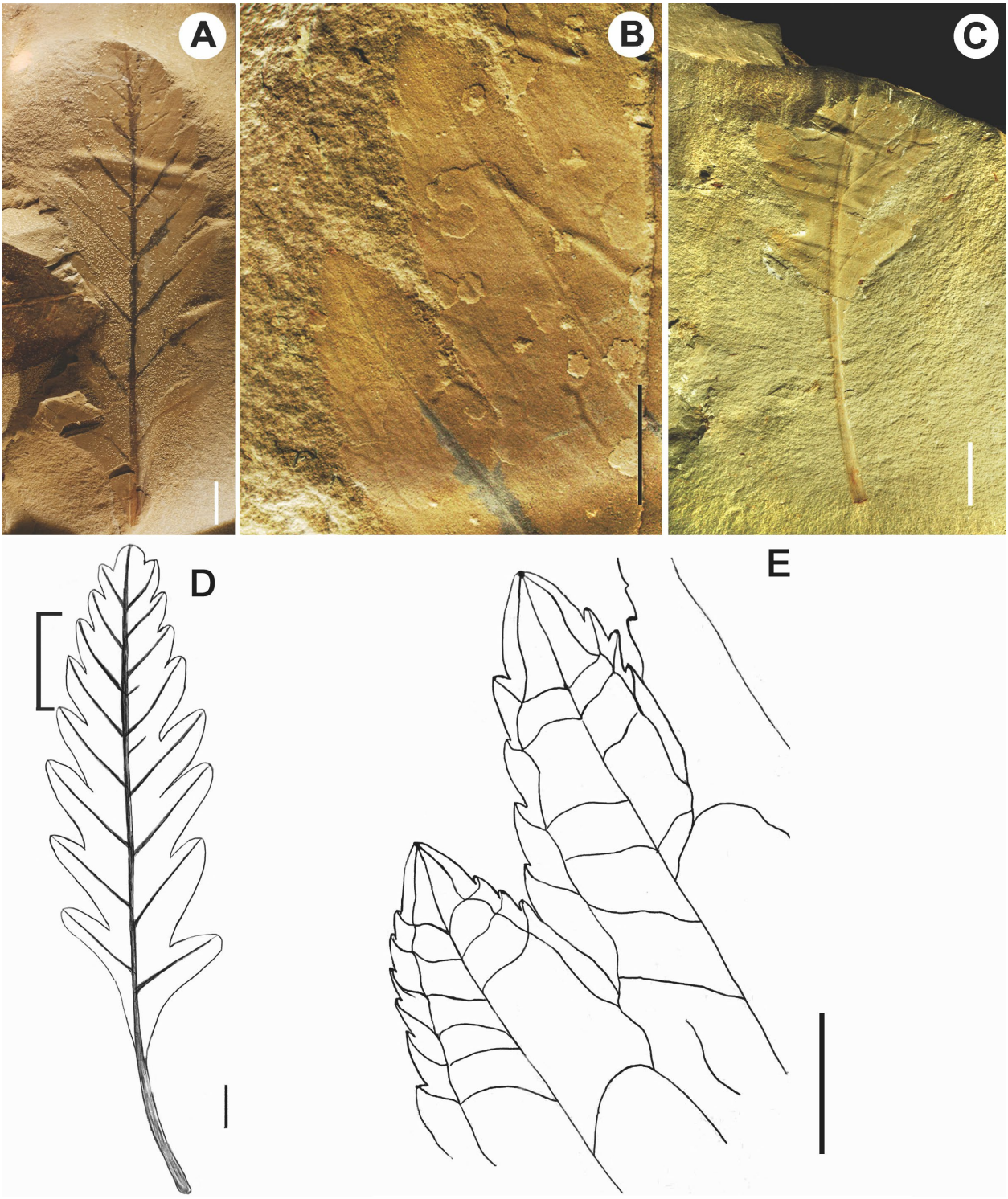

Figure 15. *Birneya lobata* gen. et sp. nov. **A**. Leaf showing distinct lateral lobes, UF 18968-61841; **B**. Enlargement of the counterpart, showing yellow gland at tip of lobes and finely serrate margin; **C**. Leaf with complete thick petiole, UF 18968-49694; **D**. Line drawing based on the lamina of specimen in A and petiole from specimen in C; **E**. Line drawing of the enlarged portion indicated by brackets in D, showing glandular teeth and higher order venation. Scale bars = 1 cm in A, C; 5 mm in B

similarities with the pinnately lobed, serrate leaves of *Crataegus*, although both available specimens of *Birneyphyllum* are larger than the laminae encountered among extant members of that genus.

Genus ***Maniastrum***
Wilder et Manchester **gen**. **nov**.

Etymology. Mani- (*L* = Morning) + astrum (*L* = Star), recognizing Chief Morning Star (c. 1810–1883) of the Northern Cheyenne People.

Plant Fossil Names Registry. PFN003513 (for generic name).

Generic diagnosis. Large, pentamerous, actinomorphic, hypogynous flower. Five free rounded sepals, each with a median cleft, ten stamens, arising in a single whorl; anthers elongate, dehiscing by slits, versatile on narrow filaments. Gynoecium unknown.

Type species. *Maniastrum decastamenus* Wilder et Manchester sp. nov.

Maniastrum decastamenus
Wilder et Manchester **sp. nov.**

Fig. 16A–I

Etymology. The epithet, *decastamenus*, refers to the ten stamens observed in these flowers.

Plant Fossil Names Registry. PFN003514 (for species name).

Specific diagnosis. Same as for genus.

Holotype here designated. UF 18968-62713 (Fig. 16A–C).

Paratypes. UF 18968-62712, 86799.

Type locality. North side of Birney, Rosebud County, Montana, USA, 45°19.53384′N, 106°30.49632′W.

Description. Flower large, 28–32 mm in diameter. Perianth actiniomorphic, hypogynous, with five free rounded sepals, 7–8 mm wide, 8–12 mm long (Fig. 16A, B, D, E, G). Stamens ten (Fig. 16F), anthers elongate, 2 mm long, 0.8 mm wide, borne on narrow filaments. Gynoecium missing (sediment-filled hollow center, 4.6–5.2 mm diameter).

Discussion. Three specimens of this flower were observed. They are faintly preserved, without much pigmentation, so could easily be overlooked despite their relatively large size. The sepals are free from each other, and each bears a median groove, although venation is not distinct. Petals were not observed, so these flowers might have been petal-less, or they may have been present but dropped prior to fossilization. Also, the gynoecium is missing, leaving a circular hole in the middle of the calyx (Fig. 16A, D, G, H), but there is an intact whorl of ten stamens. Some of the stamens are visible on the broken surface of the specimens (Fig. 16A, H, I). In addition, the full whorl of stamens is seen by X-ray within the sediment above the level of the perianth (Fig. 16F). Anthers are elongate (Fig. 16H, I) and versatile, borne on slender filaments (Fig. 16C, I). The pentamerous perianth and ten stamens indicate that this flower fits into the broad clade, Pentapetalae, but we have not resolved its familial affinity.

Genus ***Kodrulia***
Wilder et Manchester **gen nov**.

Etymology. Named for Tatiana Kodrul, recognizing her contributions to paleobotanical research on Paleocene floras.

Plant Fossil Names Registry. PFN003515 (for generic name).

Generic diagnosis. Small actinomorphic flower with narrow pedicel, five hypogynous sepals, a superior, rounded-triangular ovary, a persistent long style with trilobed stigma. Petals not seen. Base of the ovary with ten short meridional ribs.

Type species. *Kodrulia birneyensis* Wilder et Manchester sp. nov.

Kodrulia birneyensis
Wilder et Manchester **sp. nov.**

Fig. 17A–S

Etymology. The epithet refers to the town adjacent to which the fossils were collected.

Plant Fossil Names Registry. PFN003516 (for species name).

Specific diagnosis. Same as for genus.

Holotype here designated. UF 18968-62735 (Fig. 17A, B, E–M).

Paratypes. UF 18968-60411, 60419, 86796.

Type locality. North side of Birney, Rosebud County, Montana, USA, 45°19.53384′N, 106°30.49632′W.

Description. Flower actinomorphic, small, 0.5 cm long, 0.5–0.6 cm wide with narrow pedicel (Fig. 17A), five hypogynous sepals, a superior (Fig. 17E), rounded-triangular ovary (Fig. 17G, M), a persistent long style (Fig. 17E, H, N, S) with trilobed stigma (Fig. 17I). Petals were not seen. Base of the ovary showing ten ridge-like outgrowths (Fig. 17F, G, J–L, P) which may have been nectaries that alternated with the stamens.

Discussion. By reflected light, these flowers are recognizable by the combination of narrow pedicels, prominent overlapping perianth lobes and long protruding styles (Fig. 17A–D).

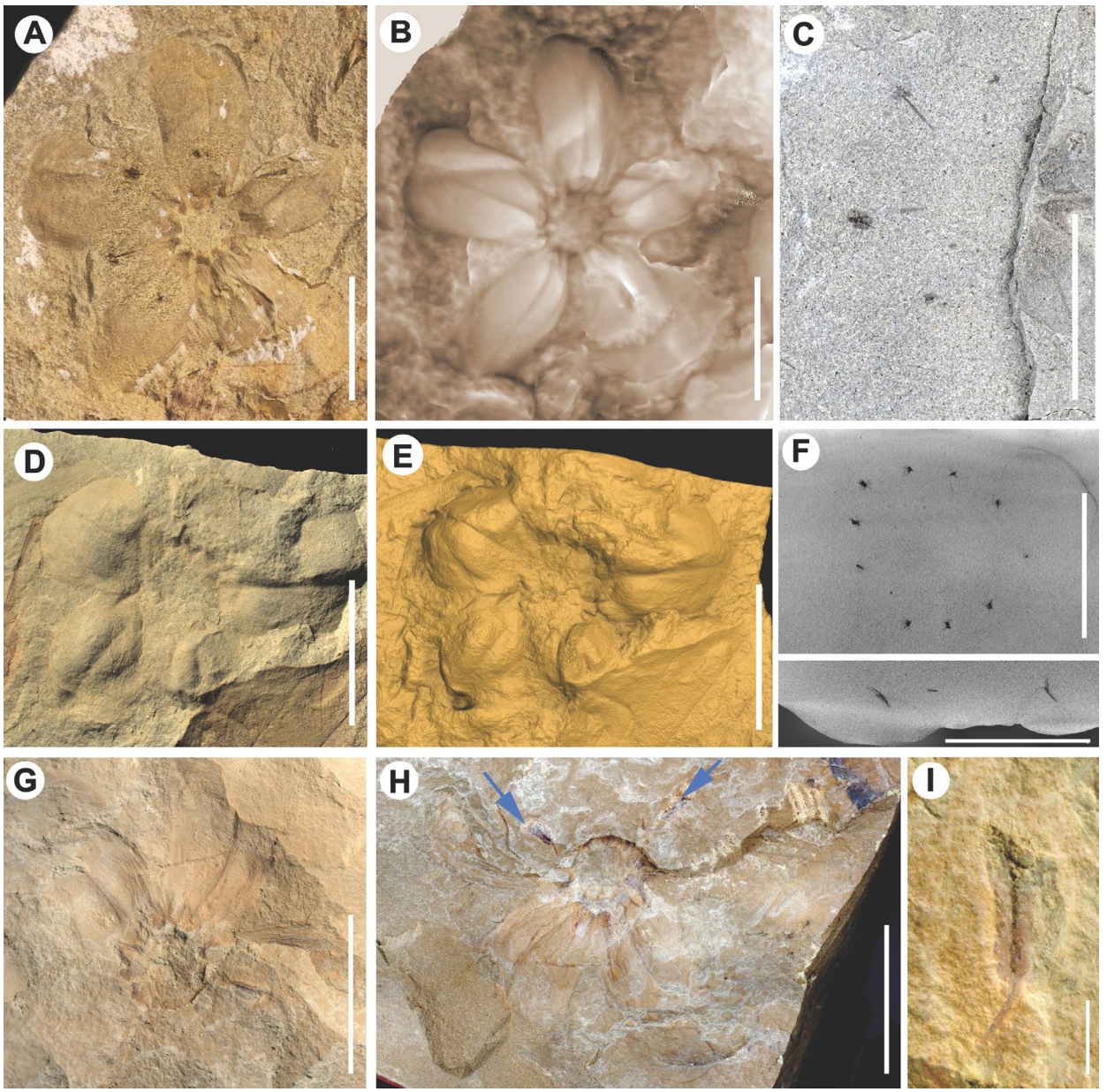

Figure 16. *Maniastrum decastamenus* gen. et sp. nov. **A–C**. Holotype, largest specimen showing the five free concave ellipsoidal tepals, each with a middle groove, a central area missing the gynoecium, surrounded by ten lobes aligned with stamens, UF 18968-62713; **A**. Reflected light imagery; composite image of both counterparts, superimposing the stamens better seen in counterpart (fig. C) in precise alignment over the primary part showing the perianth more distinctly; **B**. Depth map surface rendering from micro-CT scanning showing median groove on each tepal; base of flower toward viewer; **C**. Exposed part of the androecium showing anthers and filaments. Keyence, shadow effect reflected light; **D–G**. UF 18968-86799; **D**, **E**. Flower viewed from basal side, by reflected light (D), and surface rendering from micro-CT scanning (E); **F**. Stamens of the same flower as D, E, in virtual sections from micro-CT data. Upper image: transverse section above the perianth showing 10 stamens in a whorl. Lower image: stamens in longitudinal section showing that they are elongate, about 4 times longer than wide; **G–I**. Additional specimen, partially exposed in transverse view, reflected light, UF 18968-62712; **G**. Overall view showing at least three of the tepals (five inferred from symmetry), wide central circular area surrounded by ten staminal bases; **H**. Enlargement of the same specimen showing some stamens protruding into the sediment overlying the perianth (arrows); **I**. Filament and elongate anther of one of the stamens. Scale bars = 1 cm in A–H, 1 mm in I

The structure of the gynoecium and style are mostly hidden within the sediment and best revealed by micro-CT scanning (Fig. 17E–S). *Kodrulia* is inferred to have had three carpels based on the three stigma lobes (Fig. 17I) and trigonal form of the ovary (Fig. 17G, M). Stamens are not preserved but are inferred to have been ten in correspondence with ridges at base of the gynoecium (Fig. 17F, G, K, L, P, Q). The ridge may represent nectar glands that alternated with ten stamens. The combination of 3 carpels and a 5-merous perianth suggests affinity to the Malpighiales (Walter S. Judd, pers. comm.). *Kodrulia* warrants further study to assess its more precise affinities; we are not aware of its occurrence at other Paleocene sites.

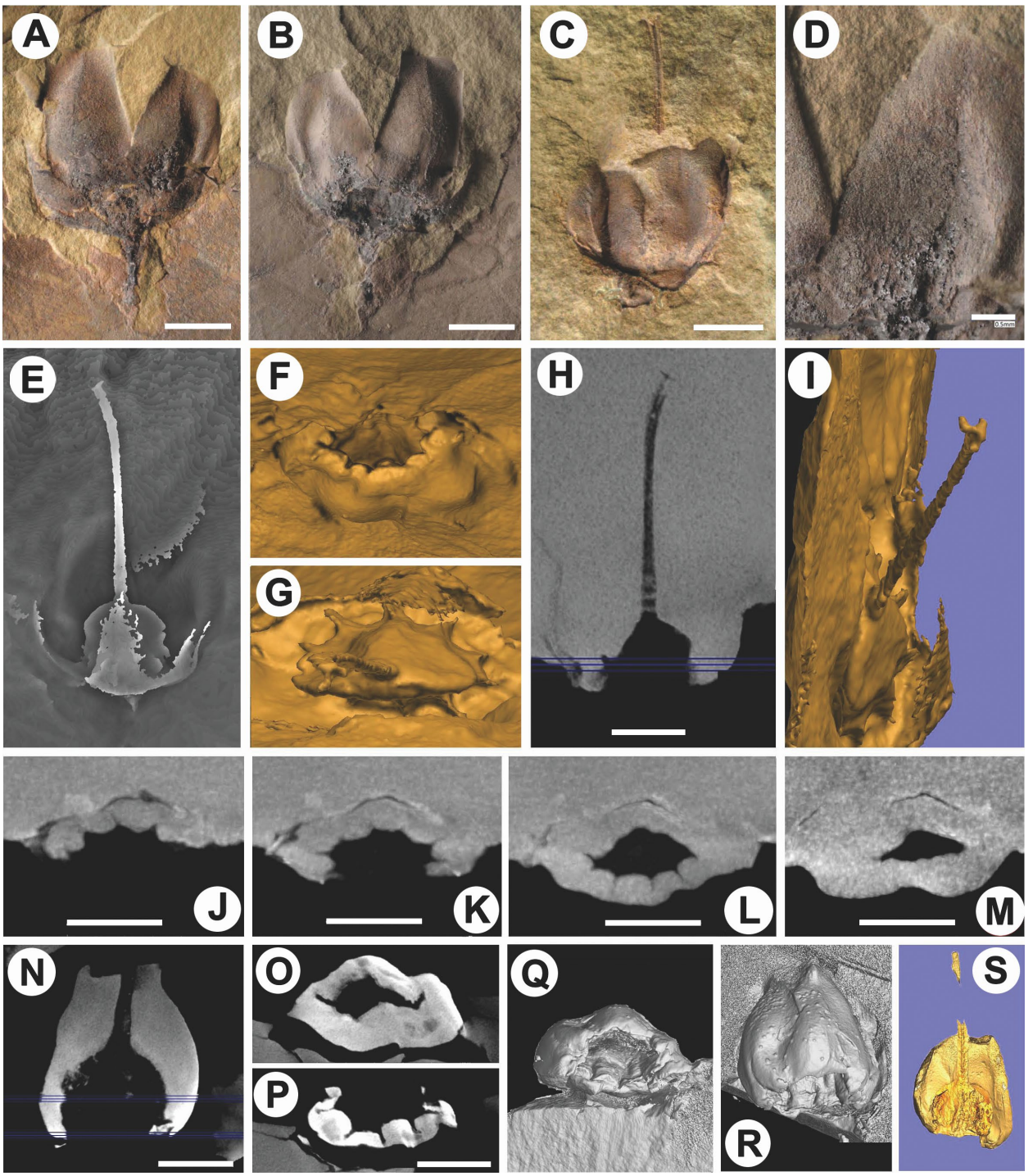

Figure 17. *Kodrulia birneyensis* gen. et sp. nov. flower. **A**, **B**. Holotype, part and counterpart UF 18968-62735, reflected light; **C**. Paratype, UF 18968-60419, reflected light; **D**. Enlargement of sepal from A. **E**–**M**. Holotype, UF 18968-62735, micro-CT scan imagery; **E**. Depth map image of flower viewed through the sediment from opposite side from A, revealing additional sepal, globose ovary, and long style; **F**. Surface rendering of the cavity at base of specimen revealing the mold of the ovary with basal radiating ribs, and three of the sepals (two more can be inferred from symmetry); **G**. Inverted imagery from F, surface rendering of the style and ovary viewed from the apex. Note ten basal ribs on the ovary; **H**. Virtual longitudinal section showing outline of the ovary and elongate style; **I**. Surface rendering from G, reoriented to lateral view, showing extended style with three stigmatic lobes; **J**–**M**. Successive transverse sections from near based of the ovary to upper ¼ of the ovary; **N**–**S**. Micro-CT scan imagery of the paratype UF 18968-86976; **N**. Virtual longitudinal section. Black areas indicate airspace, defining outline of the perianth as well as the ovary and style; **O**, **P**. Transverse sections at approximate equator of ovary (O) and in the lower ¼ with radiating ribs (P); **Q**. Surface rendering of the fruit viewed basally showing peripheral perianth and central cavity representing ovary position; **R**. Same surface rendering tilted 90° into lateral view showing apices of the sepals; **S**. Digitally extracted flower showing the ovary, protruding style and peripheral perianth. Scale bars = 2 mm

Genus ***Linguaflumenia***
Wilder et Manchester **gen nov**.

Etymology. Lingua (L = tongue) + flumen (L = river), referring to the Tongue River which flows adjacent to the town of Birney where these fossils were collected.

Plant Fossil Names Registry. PFN003517 (for generic name).

Generic diagnosis. Fruit ellipsoidal, borne on a thick, curved pedicel, and bearing an elongate persistent style. Ovary apparently superior, with about five persistent imbricate perianth remnants forming a brittle layer enclosing the ovary with apically free tips surrounding the base of the style. Style undivided, not capitate.

Linguaflumenia montanensis
Wilder et Manchester **sp**. **nov**.

Fig. 18A–H

Etymology. The epithet refers to the state of Montana.

Plant Fossil Names Registry. PFN003518 (for species name).

Specific diagnosis. Same as for genus.

Holotype designated here. UF 18968-60426 (Fig. 18A).

Paratypes designated here. UF 55392, 60417, 60418, 60420, 61844, 61845, 62736.

Other specimens included. UF 18968-49667b, 55389, 62714, 85264, 85268, 86790A, 86799.

Type locality. North side of Birney, Rosebud County, Montana, USA, 45°19.53384′N, 106°30.49632′W.

Description. This fruit type with its thick, curved pedicel, ovoid fruit body and persistent long style is distinctive and common at the Birney locality. Additional key characters include the superior ovary and the persistent apparently pentamerous accrescent perianth whorls. One specimen shows a prominent flattened appendage with well-defined longitudinal venation arising from the base of the ovary and extending apically nearly twice the length of the ovary that we interpret as a sepal, but which could alternatively be a bract (Fig. 18H). Symmetry and scar positions suggest there were originally five such sepals or bracts, although they have been lost from the other specimens. Inside the whorl of sepals, it appears that there were five imbricate petals that closely envelope the ovary with their apices surrounding the base of the style (Fig. 18A, C, E). These appear to have formed a brittle outer surface of the fruits. As yet, the affinities of this plant remain undetermined.

Genus ***Jinjianhuaia***
Wilder et Manchester **gen**. **nov**.

Etymology. The generic name recognizes Professor Jianhua Jin of Sun Yat Sen University, who aided in fieldwork at the Birney site, for his contributions to Paleogene paleobotany.

Plant Fossil Names Registry. PFN003519 (for generic name).

Generic diagnosis. Subglobose, pedicellate, loculicidal capsules, sometimes tricarpellate (3-valved), sometimes tetracarpellate (4-valved). Perianth scar hypogynous. Capsular valves opening from the apex, each with a middle longitudinal groove on the exterior of locule casts, coinciding with a septum. A short central columella protruding from base of capsule bears numerous placental projections. Capsule valves smooth, without spines. Seeds not seen.

Type species. *Jinjianhuaia birneyensis* Wilder et Manchester sp. nov.

Jinjianhuaia birneyensis
Wilder et Manchester **sp**. **nov**.

Fig. 19A–Q

Etymology. The specific epithet refers to the town of Birney, adjacent to which the fossil site is located.

Plant Fossil Names Registry. PFN003520 (for species name).

Specific diagnosis. Same as for genus.

Holotype here designated. UF 18968-60430 (Fig. 19).

Paratypes. UF 18968-35179 [3 valves], 50921, 53377 [isolated valve], 60430, 62734 [3 valves], Fig. 19O-Q], 50921 [4 valves, Fig. 19G–I],50922 [isolated valve], 62734, 85263 [4 valves, Fig. 19J–N].

Type locality. North side of Birney, Rosebud County, Montana, USA, 45°19.53384′N, 106°30.49632′W.

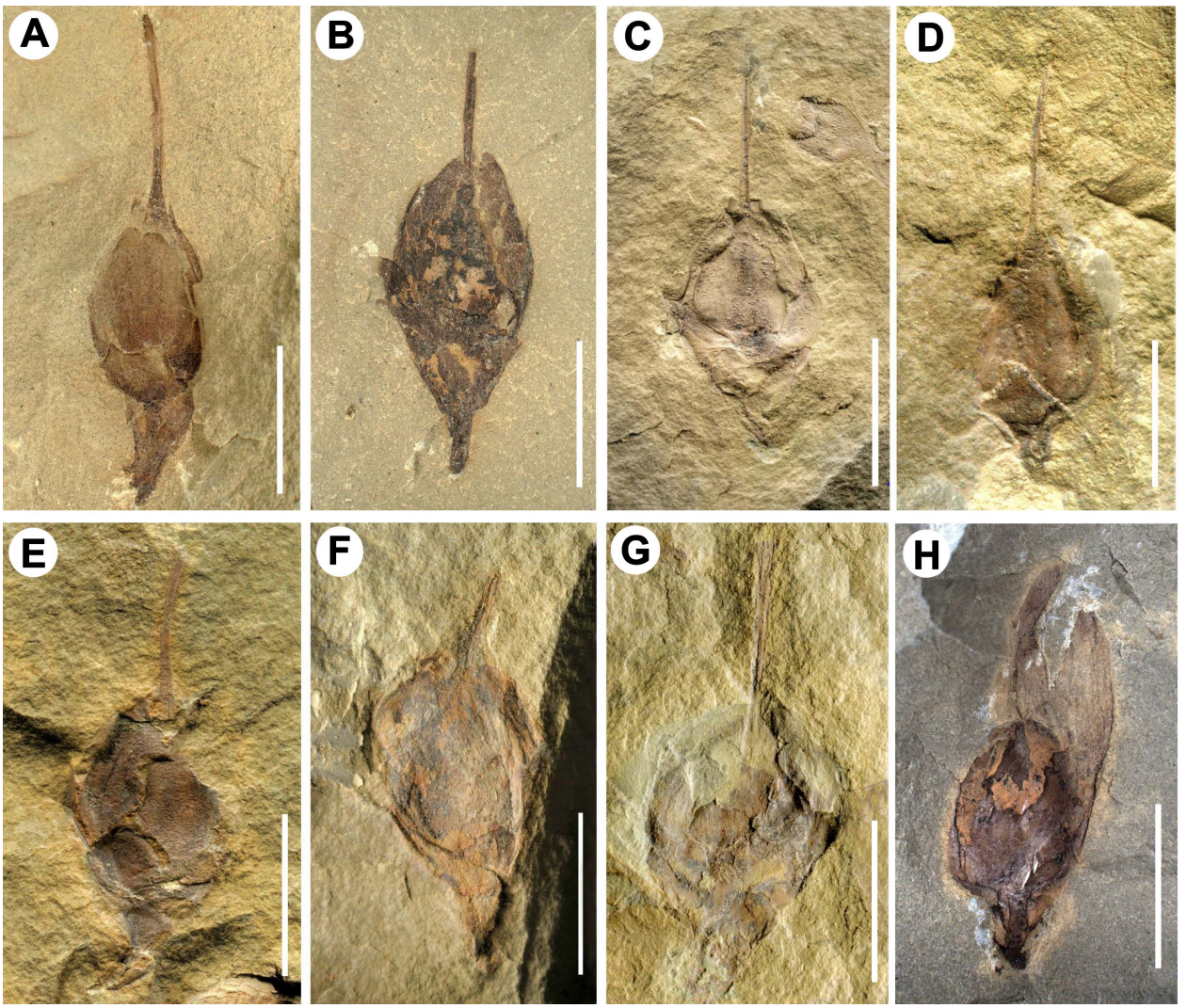

Figure 18. **A**–**H**. *Linguaflumenia montanensis* gen. et sp. nov. Several specimens showing stout pedicel, ellipsoidal fruit body, and straight persistent style; **A**. Fruit showing thick curved pedicel, ovoid fruit body, and imbricate, protruding perianth elements surrounding the base of an elongate style, holotype, UF 18968-60426; **B**. UF 18968-61844; **C**. UF 18968-55392; **D**. UF 18968-60417; **E**. UF 18968-60420; **F**. UF 18968-61845; **G**. UF 18968-62736; **H**. Specimen with a probable sepal (right side), UF 18968-60418. Scale bars = 5 mm

Description. Capsule subglobose, height 9.2–10.2 mm, width 10–13 mm. Pedicel 3.5 mm long, 1 mm thick, lacking prominent disk at junction between pedicel and capsule. Valves 5–7 mm wide. Central columella protruding from base of capsule about 1/3 the distance to apex.

Discussion. *Jinjianhuaia* fruits are loculicidal capsules varying in the number of carpels and dehiscence valves (two specimens with three valves, and at least four specimens with four valves). They bear a superficial resemblance to the capsules of *Aesculus hickeyi* which is known from other Paleocene sites in the region (Manchester, 2001), because both are loculicidal capsules of similar size with a median septal groove on the locule casts beneath each valve. However, *Jinjianhuaia* ranges from three valves to four valves, whereas *Aesculus* has only three valves. Also, the capsule valves of *A. hickeyi* have transverse wrinkles on their inner surface, and spines on the external surface, whereas capsule valves of the Birney specimens are smooth on both surfaces. Micro-CT scanning of the specimens reveals a short central column with numerous radiating projections (Fig. 19C–E, I, P) that seem to be placentae for numerous small seeds, rather than the single seed per locule of *Aesculus*.

Extant *Lagerstroemia* of the Lythraceae is similar in the morphology of its loculicidal capsular fruits, but it typically has six valves, rather than three and four. *Sloanea* of the Elaeocarpaceae also has loculicidal capsules with three to five valves. Although many

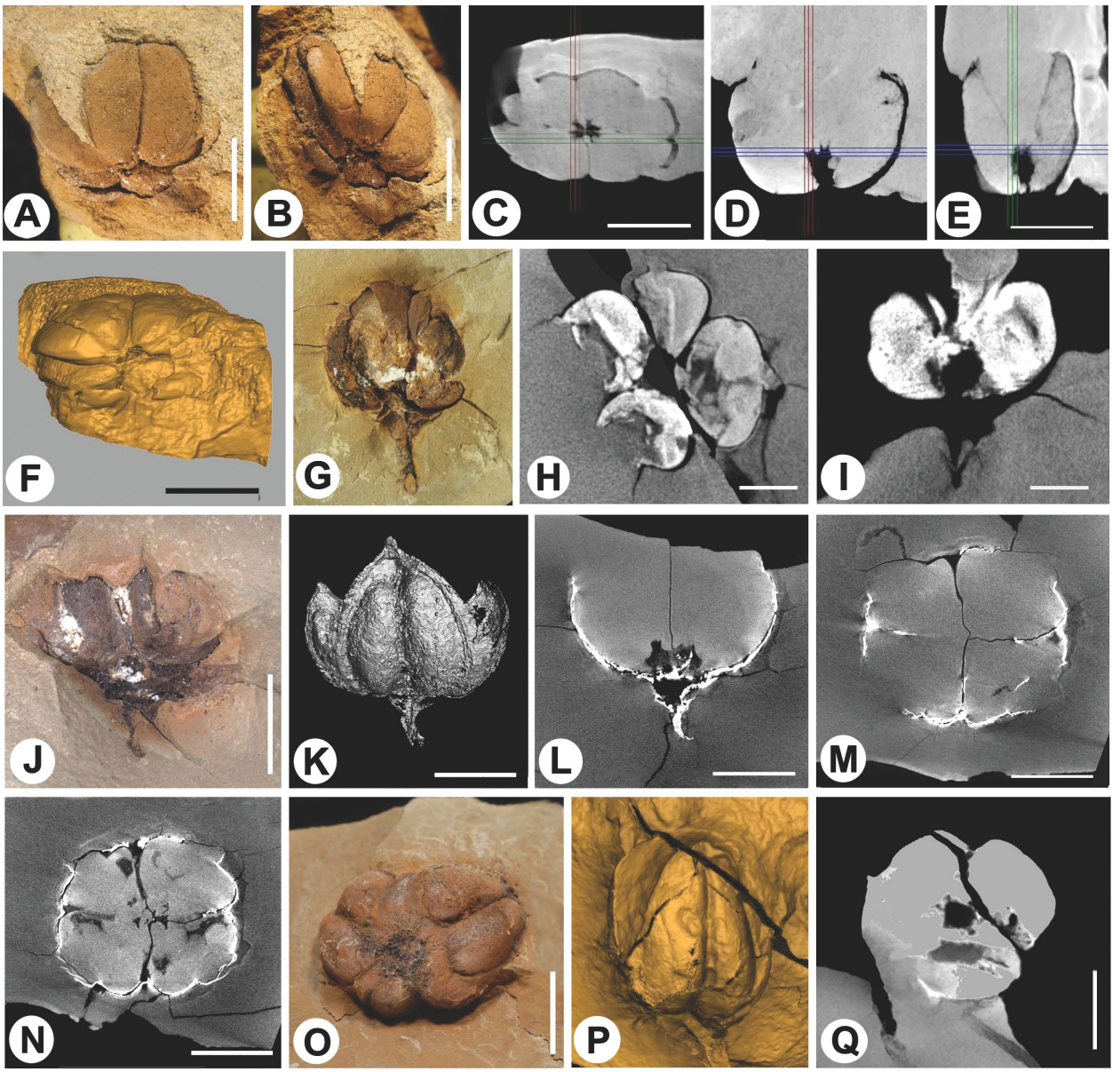

Figure 19. *Jinjianhuaia birneyensis* gen. et sp. nov. capsular fruit. **A–F**. Holotype, tetralocular fruit, UF 18968-60430; **A**, **B**. Lateral and oblique-basal view, reflected light, showing separating valves, each with a median septal cleft; **C–E**. Micro-CT scan virtual sections, with horizontal and vertical lines indicating planes of sections; **C**. Transverse section in lower 1/3, intercepting the central column and the four valves; **D**. Longitudinal section showing concave valve outlines, thin capsule walls, and short central column with remnant placentation; **E**. Longitudinal section at right angles to D. showing v-shaped apical cleft of the separating septa of two opposing valves. **F**. Basal view of same specimen surface rendering, mold surface showing smooth surface of the locule cast; **G–I**. Tetralocular fruit, UF 18968-50921; **G**. Lateral view showing pedicel, reflected light; **H**. Virtual transverse section, showing 4 locules, loculicidal dehiscence, and thick central column; **I**. Virtual longitudinal section showing bulbous short central column; **J–N**. Tetralocular fruit, UF 18968-85263; **J**. Lateral view showing pedicel, hypogynous perianth and opened capsule valves, reflected light; **K**. Surface rendering of capsule digitally extracted from sediment showing pedicel and opened valves with median septal groove; **L**. Virtual longitudinal section showing rounded surface of the opened valves.; **M**. Equatorial transverse section; **N**. Transverse section, lower 1/3; **O–Q**. Trilocular fruit, UF 18968-62734; **O**. Basal view, reflected light; **P**. lateral view, surface rendering from micro-CT data; **Q**.Virtual transverse section, showing three locules and central column with surrounding placentae. Scale bars = 5 mm

extant species and most of the fossils of this genus have spiny valves, some extant species have spineless valves. However, *Sloanea* capsules have a prominent disk at the base (Manchester and Kvaček, 2009) which is not seen in *Jinjianhuaia*. Although its placement within Eudicots is secure, the more precise affinities remain uncertain.

DISCUSSION

FLORISTIC COMPARISONS

The Birney florule differs significantly from the neighboring Horse Creek florule of similar age, located just 30 km to the east. Although both share some elements, notably

cf. *Dennstaedtia americana*, *Browniea serrata*, *Davidia antiqua*, *Nordenskioeldia borealis*, *Zizyphoides flabella*, *Trochodendroides genetrix*, *Porosia verrucosa*, and *Phyllites demoresii*, Birney is apparently lacking Taxodioid Cupressaceae, *Ulmites* Dawson, *Macginitiea* Wolfe et Wehr, *Amersinia* Manchester, Crane et Golovneva, and *Beringiaphyllum* which are well represented at Horse Creek. Conversely, Birney includes some taxa not found at Horse Creek, notably *Arthayesia*, *Birneyphyllum*, and the four newly named flower and fruit types. The occurrence of *Taxodium* Rich. and Nyssaceae at Horse Creek, as well as close proximity to coal seams, suggests a more swampy environment, whereas the Birney florule may represent streamside but not swampy vegetation.

The Birney florule shares some similarity to the Early Paleocene Ravenscrag flora of Saskatchewan, Canada, treated by McIver and Basinger (1993) and West et al. (2021). Although shared taxa are present, e.g., *Dennstaedtia americana*, *Browniea serrata*, and *Trochodendroides*, the Ravenscrag flora is strikingly more diverse, with 46 recognized plant species. West et al. (2021) used an ensemble approach to reconstruct the paleoclimate of the Ravenscrag flora. Through the leaf mass per area (M_A) analysis, all of their taxa were estimated to be deciduous, which was consistent in the Birney florule as well.

The Joffre Bridge roadcut, in Alberta, Canada, as studied by Hoffman and Stockey (2000), is a locality of Tiffanian age, with 28 plant taxa identified. This is more diverse than Birney; however, it is still relatively low in diversity much like other Tiffanian sites. Out of the taxa discovered there are two shared with Birney, cf *Dennstaedtia* and *Joffrea speirsii*, which bore leaves more or less identical to those we refer to *Trochodendroides*.

The Birney florule also includes taxa in common with those that were recorded in Hickey's (1980) biostratigraphic study of Clarks Fork Basin, about 200 km west of Birney. Although taxonomic revisions have resulted in subsequent nomenclatural changes, the shared taxa include *Aesculus* ("*Carya antiquorum*" Newberry), *Browniea* ("*Eucommia serrata*" (Newberry) Brown), cf. *Dennstaedtia americana*, *Davidia* ("*Viburnum antiquum*" (Newberry) Hollick), *Dyrana* ("*Melisoma longifolia*" (Heer) Hickey), and *Porosia verrucosa*. Hickey noted a decrease in diversity from the Puercan to Tiffanian and attributed this to a cooling in climate between those time intervals, as well as change from dominantly deciduous leaves in the Tiffanian to a higher percentage of broadleaved evergreens in the Clarkforkian, associated with an increase in mean annual temperature (Hickey, 1980).

OVERVIEW

Six genera are newly described here, not having been recorded from other sites: *Arthayesia* and *Birneyphyllum* leaves, *Maniastrum* and *Kodrulia* flowers, and *Linguaflumenia*, and *Jinjianhuaia* fruits. The two unplaced fruit types are considered as separate entities from the two unplaced flower types because their morphology is distinct, so that such fruits would not be expected to mature from either of the flower types. The maximum estimate of floristic diversity, obtained by counting the number of recognized megafossil genera (11 from leaves, plus 5 of reproductive structures including *Porosia*) is 16. As mentioned above, we think the extinct fruit genus, *Porosia*, which is very common at Birney, may coincide with the leaves of *Phyllites demoresii* because these two species co-occur at several sites in the Paleocene of Wyoming and Montana and apparently they co-occur also in far eastern Russia. The leaves called *Nyssa bureica* Krassilov from the Paleocene of the Amur Basin closely resemble those of *Phyllites demoresii*, and co-occur with *Porosia* fruits in at least three sites (Moiseeva et al., 2018). If this correlation is correct, then the number of distinct genera in the Birney florule is reduced to 15. However, there is a possibility that the two newly described leaf genera might correspond to two of the four mystery reproductive genera, so a minimal estimate of full megafossil diversity for the fossil florule as currently known (Table 1) is 13: the 11 leaf types plus two of the reproductive structures. The Birney florule includes two leaf types that have not yet been linked to reproductive structures: *Arthayesia* and *Birneyphyllum*. Could it be that the most common leaf type, *Arthayesia*, coincides with the most common fruit type, *Linguaflumenia* or perhaps to the second most abundant fruit type, *Jinjianhuaia*? To address this question, we would like to have information on co-occurrence from more sites. A single

Table 1. Taxonomic composition of the Birney florule

Taxon	Leaf	Flower	Fruit	Figure Number	Number of specimens
cf. *Dennstaedtia americana* Knowlton	+	.	.	Fig. 3A–D	9
cf. *Platanus*	.	.	+	Fig. 4E	1
Dyrana flexuosa (Newberry) Golovneva	+	.	.	Fig. 4A–D	6
Zizyphoides flabella (Newberry) Crane, Manchester et Dilcher	+	.	.	Fig. 5A–F	40
Nordenskioeldia borealis Heer	.	.	+	Fig. 6A–D	35
Trochodendroides genetrix (Newberry) Manchester	+	.	.	Fig. 7A–G	3
Corylites sp.	+	.	.	Fig. 8A–C	2
Aesculus hickeyi Manchester	+	.	.	Fig. 9A–D	21
Davidia antiqua (Newberry) Manchester	+	.	+	Fig. 10A-F	19
Browniea serrata (Newberry) Manchester et Hickey	+	.	.	Fig. 11A–E	10
Phyllites demoresii Brown	+	.	.	Fig. 12A–I	9
Porosia verrucosa (Lesqueruex) Hickey emend. Manchester et Kodrul	.	.	+	Fig. 13A–F	16
Arthayesia brevipetiolata gen. et sp. nov.	+	.	.	Fig. 14A–I	53
Birneyphyllum lobata gen. et sp. nov.	+	.	.	Fig. 15A–C	2
Maniastrum decastamenus gen. et sp. nov.	.	+	.	Fig. 16A–I	5
Kodrulia birneyensis gen. et sp. nov.	.	+	.	Fig. 17A–S	3
Linguaflumenia montanensis gen et. sp. nov.	.	.	+	Fig. 18A–H	13
Jinjianhuaia birneyensis gen et. sp. nov.	.	.	+	Fig. 19A–Q	4

fruit of *Linguaflumenia* has been observed in the Foster Gulch Late Paleocene (Clarkforkian) flora of western Montana (pers. obs. S. Manchester and S. Wing, USNM collections), but we do not know if *Arthayesia* leaves occur in that assemblage as well.

The rarest leaf in the Birney florule, represented by only two specimens, is the distinctive, pinnately lobed leaf that we have named *Birneyphyllum*. We ponder whether it may coincide with one of the two flowers unique to this site, *Maniastrum* or *Kodrulia*. The *Maniastrum* flowers and *Birneyphyllum* leaves are similar to each other in the faint impression they made in the siltstone, with hardly any trace of pigmentation remaining, contrary to other megafossils from this site that usually retain tan or brown coloration.

CLIMATIC INFERENCES

The high proportion of extinct genera in the florule precludes a statistically significant inference of climate from nearest modern relatives, but we can look to the two genera still living today for clues: *Davidia* and *Aesculus*. *Davidia*, with one species living today in central China, *Davidia involucrata* Baill. is a deciduous tree restricted to temperate climate in montane mixed forests in central and southwestern China (Ying et al., 1993), with a distribution that is delimited by precipitation, where the precipitation ranges from 0.1–58 mm in the driest month and 106–2,356 mm in the warmest quarter, and mean annual temperature, which ranges from –0.7 to 19.5°C (Long et al., 2021). *Aesculus* has a broader range of geographic distribution and climate with about 15 species today distributed around the northern hemisphere. Mostly, they are temperate, but ranging in mean annual temperature among the species from ca 9.8 (*A. indica* (Wall. ex Cambess.) Hook.) to 21.5 (*A. assamica* Griff.) (Du et al., 2020). This very broad range in mean annual temperature makes modern *Aesculus* less useful at inferring the climate of the area than *Davidia*, which has a range of mean annual temperature that is comparatively more narrow.

According to the threshold of 129 g/m^2 leaf dry mass per area (M_A) (Royer et al., 2010), all leaf types in the Birney florule were determined to likely be deciduous, with their calculated M_A (Table 2). The leaves *Davidia* and *Aesculus* were calculated to be below the threshold and deciduous, which is also true for their modern species. This points to a climate that was temperate or subtropical.

CONCLUSIONS

With only 11 leaf types among more than 250 specimens studied, the Birney florule is relatively low in diversity. There is only one kind of fern, and no gymnosperms were recovered,

Table 2. Petiole widths, lamina areas, and calculated leaf mass per area (M_A)

Taxon	# of Specimen used	Petiole width (cm)	Lamina area (cm^2)	M_A Average	Evergreen or deciduous
Dyrana flexuosa (Newberry) Golovneva	2	0.23, 0.21	111.4, 45.3	73.1	Deciduous
Zizyphoides flabella (Newberry) Crane, Manchester et Dilcher	3	0.073, 0.078, 0.053	7.2, 14.6, 1.9	77.4	Deciduous
Trochodendroides genetrix (Newberry) Manchester	1	0.095	9.8	81.4	Deciduous
Corylites sp.	1	0.12	45.8	53.94	Deciduous
Aesculus hickeyi Manchester	1	0.159	16.0	99.9	Deciduous
Davidia antiqua (Newberry) Manchester	1	0.188	34.7	84.6	Deciduous
Phyllites demoresii Brown	5	0.139, 0.085, 0.079, 0.071, 0.112	102.8, 38.1, 13.4, 24.5, 14.1	55.5	Deciduous
Arthayesia brevipetiolata gen. et sp. nov.	3	0.145, 0.081, 0.188	41.1, 18.6, 15.9	64.6	Deciduous
Birneyphyllum lobata gen. et sp. nov.	1	0.216	29.6	99.9	Deciduous

despite the presence of cupressaceous conifers at other sites of the Tongue River Member. The florule is dominated by leaves of *Zizyphoides*, *Arthayesia*, *Davidia* and *Aesculus*. The remaining leaves described herein are represented by only a few specimens. Reproductive structures are similar in diversity to the leaves. They include fruits of *Davidia*, *Nordenskioeldia*, *Platanus*, *Porosia*, *Linguaflumenia*, and *Jinjianhuaia*, seeds of Cercidiphyllaceae and flowers of *Maniastrum* and *Kodrulia*. The Birney florule has some familiar Paleocene floristic elements that were widespread during the Paleocene such as *Davidia*, *Zizyphoides*/*Nordenskioeldia*, *Trochodendroides*, *Dyrana*, *Aesculus*, and *Porosia*. Two of the genera are still surviving today (*Davidia* and *Aesculus*), but the others are apparently extinct.

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REFERENCES

APGIV (Angiosperm Phylogeny Group) 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181, 1–20. https://doi.org/10.1111/boj.12385

Bass, N.W., 1924. Coal in the Tongue River Valley, Montana. United States Geological Survey Memoirs 16748.

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, 1–116.

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.

Correa-Narvaez, J.E., Manchester, S.R., 2021. Distribution and morphological diversity of *Palaeocarpinus* (Betulaceae) from the Paleogene of the Northern Hemisphere. Botanical Review 88(2), 161–203. https://doi.org/10.1007/s12229-021-09258-y

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, 1311–1334. https://doi.org/10.1002/j.1537-2197.1991.tb12599.x

Du, Z.Y., Harris, A.J., Xiang, Q.Y.J., 2020. Phylogenomics, co-evolution of ecological niche and morphology, and historical biogeography of buckeyes,

horse chestnuts, 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, 106726. https://doi.org/10.1016/j.ympev.2019.106726

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.

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. University of Michigan Papers in Paleontology 24, 33–49.

Hoffman, G.L., Stockey, R.A., 2000. Geological setting and paleobotany of the Joffre Bridge Roadcut fossil locality (Late Paleocene), Red Deer Valley, Alberta. Canadian Journal of Earth Sciences 36(12), 2073–2084. https://doi.org/10.1139/e99-095

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

Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F., Donoghue, M.J., 2016. Plant Systematics: A Phylogenetic Approach. Sinauer Associates Inc., Sunderland, MA. https://doi.org/10.1093/hesc/9781605353890.001.0001

Knowlton, F.H., 1910. Descriptions of fossil plants from the Mesozoic and Cenozoic floras of North America. Smithsonian Miscellaneous Collections 52(4), 489–496.

Kvaček, Z., 2008. Whole-plant reconstructions in fossil angiosperm research. International Journal of Plant Sciences 169(7), 918–927. https://doi.org/10.1086/589694

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., 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.

Manchester, S.R., 2014. Revisions to Roland Brown's North American Paleocene flora. Acta Musei Nationalis Pragae, Ser. B – Historia Naturalis 70(3–4), 153–210.

Manchester, S.R., Chen, Z.D, 1996. *Palaeocarpinus aspinosa* sp. nov. (Betulaceae) from the Paleocene of Wyoming, USA. International Journal of Plant Sciences 157(5), 644–655. https://doi.org/10.1086/297386

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 167(4), 897–908. 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., Kvaček, Z., 2009. Fruits of *Sloanea* (Elaeocarpaceae) in the Paleogene of North America and Greenland. International Journal of Plant Sciences 170(7), 941–950. https://doi.org/10.1086/600148

Manchester, S.R., Crane, P.R., Dilcher, D.L., 1991. *Nordenskioeldia* and *Trochodendron* (Trochodendraceae) from the Miocene of northwestern North America. Botanical Gazette 152, 357–368. https://doi.org/10.1086/337898

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. (J.), Kodrul, T.M., Akhmeiev, 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

Manchester, S.R., Calvillo-Canadell, L., Cevallos-Ferriz, S.R., 2014. Assembling extinct plants from their isolated parts. Boletín de la Sociedad Geológica Mexicana 66(1), 53–63.

Manchester, S.R., Foster, A., Lott, T.A., 2023. The Paleocene Horse Creek florule, Tongue River Member of the Fort Union Formation, southeastern Montana, USA. Acta Palaeobotanica 63(1), 32–53. https://doi.org/10.35535/acpa-2023-0003

Mapel, W.J., 1976. Geologic map and coal sections of the Birney Quadrangle, Rosebud County, Montana. United States Geological Survey Miscellaneous Field Studies Map 813.

Mapel, W.J., Martin, B.K., Butler, B.A., 1978. Coal resource occurrence and coal development potential maps of the Poker Jim Butte Quadrangle, Rosebud and Powder River counties, Montana. United States Geological Survey Open-File Report 78-651, 1–26.

McIver, E.E., Basinger, J.F., 1993. Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. Palaeontography of Canada 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

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. https://doi.org/10.2475/102011.01

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. https://doi.org/10.2307/3514576

Royer, D.L., Sack, L., Wilf, P., Lusk, C.H., Jordan, G.J., Niinemets, Ü., Wright, I.J., Westoby, M., Jordan, G.J., Niinemets, U., Coley, P.D., Cutter, A.D., Labandeira, C.C., Palmer, M.B., Johnson, K.R., Moles, A.T., Valladares, F., 2007. Fossil leaf economics quantified: Calibration, Eocene case study, and implications. Paleobiology 33, 574–589. https://doi.org/10.1666/07001.1

Royer, D.L., Miller, I.M., Peppe, D.J., Hickey, L.J., 2010. Leaf economic traits from fossils support a weedy habit for early angiosperms. American Journal of Botany 97, 438–445. https://doi.org/10.3732/ajb.0900290

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, 110488, 14 pp. https://doi.org/10.1016/j.palaeo.2021.110488

Ying, T-S, Zhang, Y.-L, Bouford, D.E., 1993. The endemic genera of seed plants of China. Science Press, Beijing.

Zolina, A.A., Manchester, S.R., Golovneva, L.B., 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