

# The mid-Paleocene fruit and seed flora from the Fort Union Formation of Newell's Nook, southeastern Montana, USA

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**ABSTRACT.** The middle Paleocene Newell's Nook biota of the Tongue River Member of the Fort Union Formation, southeastern Montana, is best known for its early Tiffanian mammalian fauna. Here, we describe an informative fruit and seed assemblage from this locality. These records refine the lower stratigraphic boundary for several plant genera known more widely from the Fort Union paleobotanical localities of less certain stratigraphic assignment within the upper Paleocene and help to fill a gap in our knowledge about the mid-Paleocene floristic composition of the Rocky Mountain and Great Plains region. Recognized plant taxa belong to the families Characeae, Taxaceae, Menispermaceae, Sabiaceae, Hamamelidaceae, Cercidiphyllaceae, Vitaceae, Cucurbitaceae and Juglandaceae. Several morphotypes remain uncertain as to familial position. Based on the dispersal syndromes of extant relatives, about 2/3 of these fruits were adaptive for animal dispersal, with hard seeds or endocarps covered by a fleshy outer layer. Dry seeds and nuts were likely part of the diet of small mammals. The Newell's Nook locality presents another rare example of a North American Paleocene fruit and seed locality and provides insights to the dietary habits and ecology of the co-occurring fauna of this time.

**KEYWORDS:** Brassicales, carpoflora, Cucurbitales, Tiffanian, *Jenkinsella*

## INTRODUCTION

Paleocene floras in North America are primarily known from assemblages of leaves (Brown, 1962; Hickey, 1977; Gemmill and Johnson, 1997; Ellis et al., 2003; Stockey et al., 2013; Manchester, 2014) and pollen (Stanley, 1965; Pocknall and Nichols, 1996; Zetter et al., 2011). Fossil fruits and seeds can provide greater systematic resolution than leaves and pollen but – because of their rarity – are often studied as accessories to foliage treatments (Brown, 1962; Hickey, 1977) or in treatments of particular taxonomic groups (e.g. Trochodendraceae, Platanaceae, Betulaceae, Juglandaceae, Sapindaceae, Cornaceae, Nyssaceae, Icacinaceae, Elaeocarpaceae). In North America, the only Paleocene

fruit and seed assemblages described to date are those of the late Paleocene (likely late Tiffanian) site near Almont, North Dakota (Crane et al., 1990) and the early Paleocene (early Puercan) site from Littleton Colorado (Huegele and Manchester, 2020). Here we describe a new assemblage of fruits and seeds from a mid-Paleocene (early Tiffanian) site in southeastern Montana: the Newell's Nook flora.

The Newell's Nook site is located in the northern Powder River Basin, Montana, within the Tongue River Member of the Fort Union Formation. This locality has yielded a rich fauna of fish, turtles, crocodiles and a diversity of mammals including at least 21 species and at least 17 families (Robinson and Honey, 1987). The mammalian fauna indicates an

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early Tiffanian (or possibly latest Torrejonian) age – placing this site in the middle Paleocene (Robinson and Honey, 1987). Palynology was previously investigated for this locality in an unpublished US Geological Survey report from July 7, 1992, by Douglas Nichols. In that report, Nichols stated that the palynoflora coincides with palynological Zone P3 of Nichols and Ott (1978). Juglandaceous pollen dominates the assemblage; this includes *Momipites actinus*, *M. leffingwellii*, *M. ventifluminis*, *M. wyomingensis* and *Caryapollenites prodromus*. Other common pollen taxa include *Alnipollenites* and *Triporopollenites* (Betulaceae), *Ulmipollenites* sp. (Ulmaceae), and *Retitrescolpites* sp. (Platanaceae). The assemblage also includes the sapindaceous or myrtaceous *Insulapollenites rugulatus*, the important K-Pg taxon *Aquilapollenites spinulosus*, taxodioid Gymnosperm pollen, fern spores and *Sphagnum* moss spores.

In this article, we document the diversity of fruit and seed types currently known from the Newell's Nook locality. These fossil disseminules, recovered along with the teeth and bone material by screen-washing, give us insight into the vegetation that hosted these mid-Paleocene animals. The results presented here include recognition of new occurrences of Characeae, Taxaceae, Menispermaceae, Hamamelidaceae, Vitaceae, Juglandaceae, Cucurbitaceae, Lythraceae, Rutaceae and Nysaceae, as well as extensions in geographic range of genera (e.g. *Kingsboroughia rostrelata*, *Jenkinsella*) previously documented from the Paleocene of North America.

## MATERIALS AND METHODS

A collection of 65 paleobotanical specimens were loaned for study by Laura Robinson and the late James Honey of the US Geological Survey in Denver. These specimens are now housed at the National Museum of Natural History, Washington, DC (USNM). The fossil fruits and seeds were recovered as a byproduct of vertebrate fossil recovery efforts from the Newell's Nook locality, which is situated in the Tongue River Member of Fort Union Formation, about 48 km east of Hardin, Big Horn County Montana (E 1/2 sec. 12, T. 2 S., R. 37 E; the center point of the E1/2 of indicated section is 45.672452°N, 107.086672°W). Specimens were extracted from a clay clast conglomerate, which was soaked in kerosene for a few days prior to sieving. The fossils are preserved as siltstone casts and mostly lack internal anatomy, but they sometimes retain cellular details of the external surface permineralized in limonite or siderite. Recrystallization may have distorted

morphology in some specimens, making it difficult to interpret internal anatomy.

Specimens were photographed with a Nikon Coolpix 995 camera or a Canon EOS 450d SLR camera mounted on a Nikon SMZ10 dissecting microscope. Lighting was adjusted using fiber optics for high contrast or small incandescent bulbs on flexible shafts for more diffuse lighting. Additional imagery was obtained by micro-computed tomography ( $\mu$ CT) scans at the Nanoscale Research Facility, College of Engineering, University of Florida. We used a GE Phoenix V|tome|x240 CT scanner with a tungsten reflection target to make scans at different resolutions with the following settings: (1) voltage of 210 kV, and a current of 120  $\mu$ A, producing a scan with 1400 images at a voxel size of 0.02641095 mm; (2) voltage of 120 kV, and a current of 80  $\mu$ A, producing a scan with 2200 images at a voxel size of 0.00933466 mm; and (3) voltage of 120 kV, and a current of 60  $\mu$ A, producing a scan with 2200 images at a voxel size of 0.00769446 mm. These scans were processed in VGStudioMax (ver. 3.1; Volume Graphics, Charlotte, NC), Avizo (ver. 9.0.0; FEI Visualization Science Group, Hillsboro, OR), and Meshlab (Cignoni et al., 2008). Imagery from VGStudioMax was produced in the same manner as in Huegele and Manchester (2019, 2020), for isosurface renderings, volume renderings and virtual sections through the disseminules. The original TIFF stacks from these scans and other derived imagery and animations can be found at <https://www.morphosource.org/projects/00000C858>.

## RESULTS

At least 13 different species are represented in the assemblage, nine of which could be identified to a modern family and/or genus. Table 1 lists the recognized taxa from Newell's Nook. In the following paragraphs, we provide a summary for each of the represented species, organized in systematic order after the Angiosperm Phylogeny Group (APGIV).

### CHAROPHYTES

#### Order CHARALES

#### Family CHARACEAE

#### Tribe NITELLEAE

#### Genus indet.

Pl. 1, fig. 1

Specimens. USNM 728257 (set of 8 specimens under this number).

Remarks. The Newell's Nook oospores are globose, have a rounded apex and base,

**Table 1.** Paleocene Carpoifloras of North America

Newell's Nook, Montana	Other Localities in the Tongue River Member	Almont, North Dakota	Sand Draw, Wyoming*	Littleton, Colorado
Taxaceae <i>cf. Taxus</i> <i>Diploporus</i>			Taxaceae <i>Diploporus</i>	
		Taxodiaceae <i>cf. Parataxodium</i>		
		Ginkgoaceae <i>Ginkgo</i>	Ginkgoaceae	
			Cupressaceae (?)	
			Magnoliaceae <i>Magnolia</i>	
			Annonaceae <i>Annonaspermum</i>	
Menispermaceae <i>Palaeoluna</i>		Menispermaceae <i>cf. Canticocculus</i>	Menispermaceae Palaeosinomenium (?) Tinospora (?)	
Sabiaceae <i>Kingsboroughia</i> <i>rostellata</i>		Sabiaceae <i>K. rostellata</i>	Sabiaceae <i>Kingsboroughia</i> / <i>Meliosma</i>	Sabiaceae <i>K. rostellata</i>
		Platanaceae	Platanaceae <i>Platanus</i>	
	Trochodendraceae <i>Nordenskioldia</i>	Trochodendraceae <i>Nordenskioldia</i>	Trochodendraceae <i>Concavistylon</i>	
Hamamelidaceae		Hamamelidaceae <i>Hamawilsonia</i> (Benedict et al., 2008)	Hamamelidaceae	
Hamamelidoideae				
Cercidiphyllaceae <i>Jenkinsella</i>		Cercidiphyllaceae <i>Jenkinsella</i>		
Vitaceae <i>Vitis</i>			Vitaceae <i>Ampelocissus</i>	
		Ochnaceae <i>Paleochna</i> (Ickert-Bond et al., 2015)		
	Cannabaceae <i>Celtis</i>			
Juglandaceae <i>Polyptera</i>		Juglandaceae <i>Cyclocarya</i>	Juglandaceae <i>Cyclocarya</i>	
		Betulaceae <i>Palaeocarpinus</i>	Betulaceae <i>Cranea</i>	
Cucurbitaceae <i>Libasperma</i>				
Lythraceae <i>Decodon</i>				
	Sapindaceae <i>Aesculus</i>			
Rutaceae <i>Zanthoxylum</i> <i>Phellodendron</i>				
			Ericales Indet. capsular species Symplocaceae <i>Symplocos</i> (?)	
Cornales Nyssaceae	Cornales <i>Amersinia</i> <i>Browniea</i> <i>Davidia</i>	Cornales <i>Amersinia</i> <i>Cornus</i>	Cornales <i>Davidia</i> <i>Langtonia</i> <i>Mastixia</i>	Cornales <i>Amersinia</i> <i>Langtonia</i> <i>Mastixicarpum</i> <i>Portnallia</i>
		Icacinaceae <i>Palaeophytocrene</i>	Icacinaceae <i>Iodes</i> <i>Palaeophytocrene</i>	
References		Benedict et al., 2008; Crane et al., 1990; Ickert-Bond et al., 2015	Tiffney and Manchester, 2019	Huegele and Manchester, 2020

\* List of Sand Draw taxa referenced from Tiffney and Manchester (2019 Abstract)

a circular basal plate, and 6–8 convolutions visible in lateral view. They are ~0.4–0.7 mm in diameter. Characeae oospores, also known as gyrogonites when calcified (Soulié-Märsche and García, 2015), are easily recognized by their small size, cylindrical or ellipsoid form, and spiraled ornamentation. The number of sister cells is useful for identifying oospores as tribe Characeae vs. tribe Nitelleae, however, these sister cells are not easily observable in the Newell's Nook specimens. The almost spherical shape of these oospores is reminiscent of many oospores of tribe Nitelleae, but these likely do not have affinities with *Nitella* itself, which has laterally compressed oospores. This is unlike the oospores of other Characeae; for example, *Lamprothamnium* are cylindrical and have a flat apex and base (Soulié-Märsche and García, 2015). The Newell's Nook fossils likely represent the morphology of the oospore itself and not the outer, often rough, calcified surface of the gyrogonite; the outer surface of the gyrogonite may have been broken off and lost with the matrix material during sieving.

## GYMNOSPERMS

### Order PINALES

#### Family TAXACEAE

##### Genus *Diploporus* Manchester

Pl. 1, fig. 2

Specimen. USNM 728214.

Remarks. *Diploporus* is represented at Newell's Nook by a single incomplete seed cast which is clearly recognizable by an approximate 1:1 length/width ratio, two planes of symmetry, elliptical outline in face view, ovate outline in lateral view, lensoidal outline in transverse view, and a pair of prominent equatorial pores and an apical keel in the major plane of bisymmetry. *Diploporus*, initially described from the Middle Eocene of Oregon (Manchester, 1994), is an extinct genus with similarities to seeds of *Torreya*. The genus is common in the Paleocene Almont flora of North Dakota (categorized as "Globose Fruit with Irregular Surface Pits" in the preliminary treatment by Crane et al., 1990, their fig. 25j).

##### Genus cf. *Taxus* L.

Pl. 1, figs 3, 4

Specimens. USNM 726254 (Pl. 1, fig. 3), 728233 (Pl. 1, fig. 4).

Remarks. Seeds of the yew tree, *Taxus*, have a truncate base marked by an elliptical scar, representing the position of aril attachment, a lensoidal cross section, and a pair of prominent vascular bundles running longitudinally inside the lateral margins of the seed. These specimens are ovate, sharply pointed at apex, bluntly truncated at base, and lensoidal or elliptic in cross section. The lateral margin is keeled in the major plane of symmetry. The surface is smooth or roughly ornamented by longitudinal ridges. USNM 728254 bears a prominent depression, which may represent biotic damage. The Newell's Nook specimens are infillings of the seed coat. Their outer layer is removed so that the pair of ascending lateral bundles is seen as grooves along the lateral keels rather than being fully hidden within the seed coat. Although these morphological features suggest affinities with *Taxus*, we refer to these seeds as cf. *Taxus* because of their small size. Better preserved examples of fossil *Taxus*, with permineralized seed coat, were recognized from the middle Eocene of Oregon (Manchester, 1994).

## ANGIOSPERMS

### Order RANUNCULALES

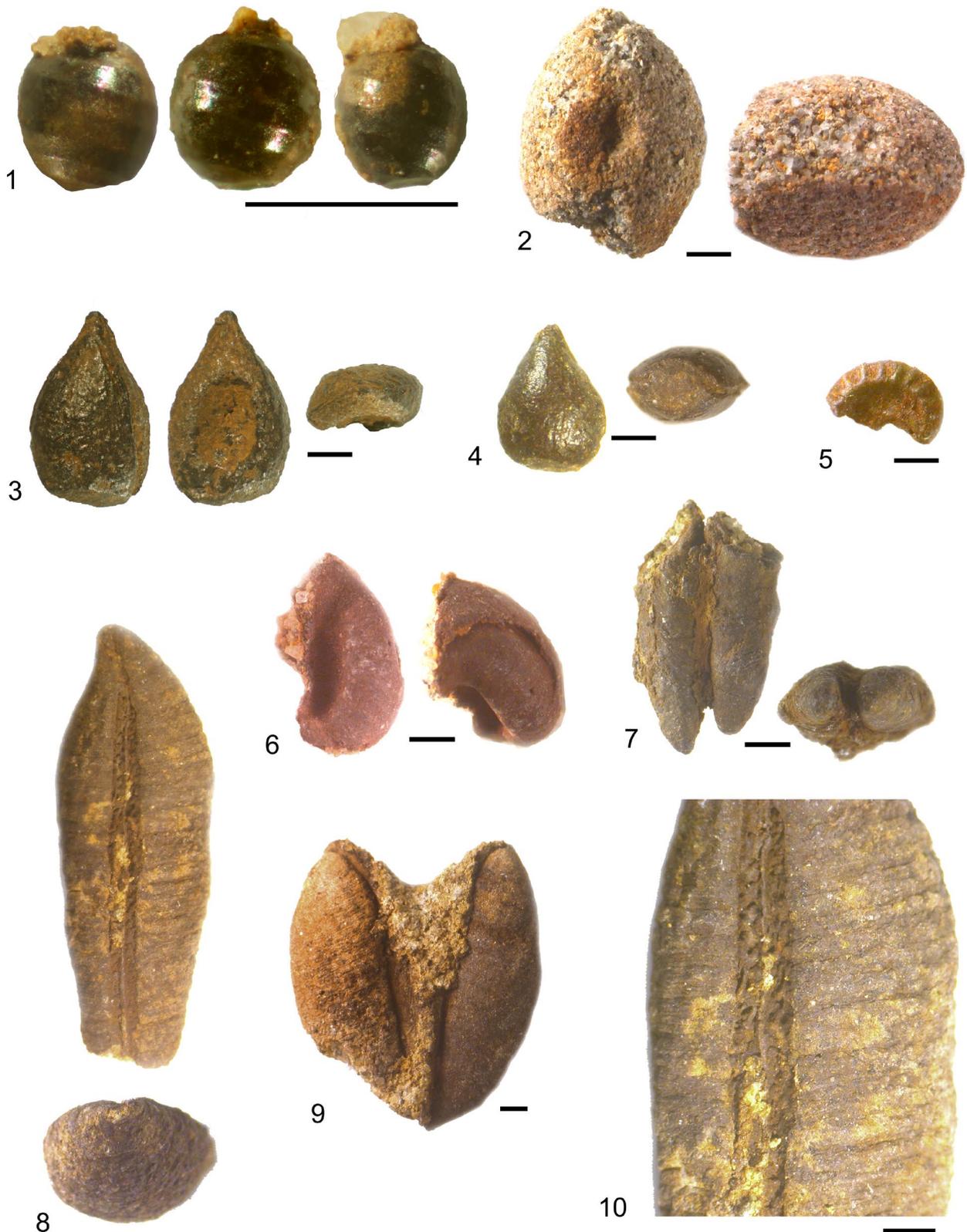
#### Family MENISPERMACEAE

##### Genus *Palaeoluna* Herrera, Manchester, Hoot, Wefferling, Carvalho et Jaramillo

Pl. 1, fig. 5

Specimen. USNM 728217.

Remarks. A single broken locule cast exhibits the distinctive horseshoe morphology and fluted sculpture of the moonseed family. *Palaeoluna* is recognizable by its unequal locule limbs and lack of radial ridges. This genus was described from the Paleocene Fort Union Formation of Linch, Wyoming, and the Paleocene Bogotá Formation of Cundinamarca, Colombia, by Herrera et al. (2011). *Palaeoluna* has many similarities to *Palaeosinomenium*, which is known from the Eocene of England, Germany and Oregon (Chandler, 1961; Manchester, 1994).



**Plate 1.** Fruits, seeds, and oospores from the Newell's Nook flora. **1.** Characeae oospores, USNM 728257. Note spiral cells, which form 6–8 convolutions in these fossils; **2.** *Diploporous* seed, USNM 728214; **3, 4.** cf. *Taxus* seeds. Note grooves in lateral margin of specimen in 4, indicating location of lateral vascular bundles; **3.** USNM 726254; **4.** USNM728233; **5.** *Palaeoluna* endocarp, USNM 728217. Note unequal development of locule limbs; **6.** *Kingsboroughia rostellata* endocarp showing a ventral scar and dorsal keel, USNM 728218; **7.** Hamamelidaceae subfamily Hamamelidoideae locule cast of a bilocular capsule, USNM 728238; **8–10.** *Jenkinsella* pods showing transverse striations; **8, 10.** Isolated pod, USNM 728231; **9.** Paired pod, USNM 728232. Scale bars = 1 mm

## Order PROTEALES

## Family SABIACEAE

## Subfamily MELIOSMOIDEAE Mast.

Genus *Kingsboroughia* Liebm.Species *Kingsboroughia rostellata*  
(Lesquereux) Huegele et Manchester

Pl. 1, fig. 6

Specimen. USNM 728218.

Remarks. A single broken endocarp confirms the presence of Sabiaceae. The specimen bears a dorsal longitudinal keel and prominent ventral scar, characteristic of *Kingsboroughia* and *Meliosma*. The smooth surface and lack of a ventral protrusion conforms with *Kingsboroughia*. The Newell's Nook specimen is similar in size and shape to *K. rostellata* previously recognized from Colorado and North Dakota (Crane et al., 1990; Huegele and Manchester, 2020).

## Order SAXIFRAGALES

## Family HAMAMELIDACEAE

## Subfamily HAMAMELIDOIDEAE

## Genus indet.

Pl. 1, fig. 7

Specimen. USNM 728238.

Remarks. One specimen represents a conjoined locule cast of a bilocular capsule of Hamamelidaceae subf. Hamamelidoideae. Well-preserved racemes of capsular hamamelidaceous fruits were described from the Almont flora (*Hamawilsonia*; Benedict et al., 2008). The specimens from Newell's Nook are smaller, but share characteristics of the Hamamelidoideae subfamily, which have bilocular capsules with explosive seed dehiscence (Endress, 1989; Li, 1997). Like most Hamamelidoideae, the Newell's Nook fruits are bilaterally symmetrical, elliptic in face view, elliptic in transverse view, and truncate apically.

## Family CERCIDIPHYLLACEAE

Genus *Jenkinsella* Reid et Chandler

Pl. 1, figs 8–10

Specimens. USNM 728223 to 728230, 728231 (Pl. 1., fig. 8, 10), 728232 (Pl. 1, fig. 9).

Remarks. Fruits of *Jenkinsella* are represented by isolated and paired pods. These pods were commonly referred to under the fossil genus *Nyssidium* Heer (e.g. Crane, 1984; Feng et al., 2000), however, the type species of that genus from Spitsbergen does not coincide with the *Cercidiphyllum*-like fruits subsequently attributed to that genus. Thus, the later established generic name, *Jenkinsella*, has priority (Golovneva and Alekseev, 2010, 2017). *Jenkinsella* was first described from the Early Eocene London Clay flora (Reid and Chandler, 1933). Brown (1939) placed these in the extant genus *Cercidiphyllum* based on similarities in the morphology of their pods, winged seeds, and associated leaves. *Jenkinsella* differs, however, from extant *Cercidiphyllum* in terms of size, attachment, orientation of striations on the fruit wall and their racemose rather than clustered infructescences (Crane, 1984). The earliest records of Cercidiphyllaceae (*Jenkinsella filatovii* fruits and their associated leaves, *Trochodendroides potomacensis*) date to the Albian of Siberia (Golovneva and Alekseev, 2010, 2017). The greatest morphological diversity of *Cercidiphyllum*-like plants occurred during the Turonian-Coniacian and the late Paleocene to early Eocene (Brown, 1939). Some representatives of these plants have been reconstructed in considerable detail (e.g. *Joffrea speirsii*; Crane and Stockey, 1985). Similar fruits are known from the late Cretaceous, e.g. the Hell Creek Formation, to the Eocene, e.g. the Clarno Formation of Oregon (Wheeler and Manchester, 2014). *Jenkinsella* produced distinctive winged seeds, which have been found in situ within fruits from London Clay and seen dispersed at many sites where the fruits also occur (e.g. Pl. 54, dif. 5, 15–17 in Brown, 1939; Text-fig. 7.5 in Manchester, 2014).

## Order VITALES

## Family VITACEAE

Genus *Vitis* L.

Pl. 2, fig. 1

Specimen. USNM 728219.

Remarks. The grape family is represented in the Newell's Nook flora by a single seed cast, showing a centrally placed, circular dorsal chalaza and a pair of ventral infolds. The seed is

~3 mm high and 3 mm wide, subglobose, bilaterally symmetrical, obovate in dorsiventral view. The apex is slightly concave and the base (hilar end) broadly rounded, ventral infolds are straight, slightly divergent. The outline of the chalaza is circular, confined to the center of the dorsal side. It resembles *Vitis* more than *Ampelopsis* because of its chalazal-apex groove (Chen and Manchester, 2011). This specimen closely resembles the *Vitis* sp. seed illustrated by Brown (1962: pl. 53, fig. 5) from the Fort Union Formation in the Shotgun Butte area of central Wyoming (USGS loc. 9132). Although similar in size to the seed of *Ampelocissus* from the late Paleocene Silica Summit Butte site at Beicegal Creek, North Dakota, the ventral infolds of that species are cup-like, rather than

slit-like (Chen and Manchester, 2007). Apparently, both genera were present in the Paleocene of this region.

### Order FAGALES

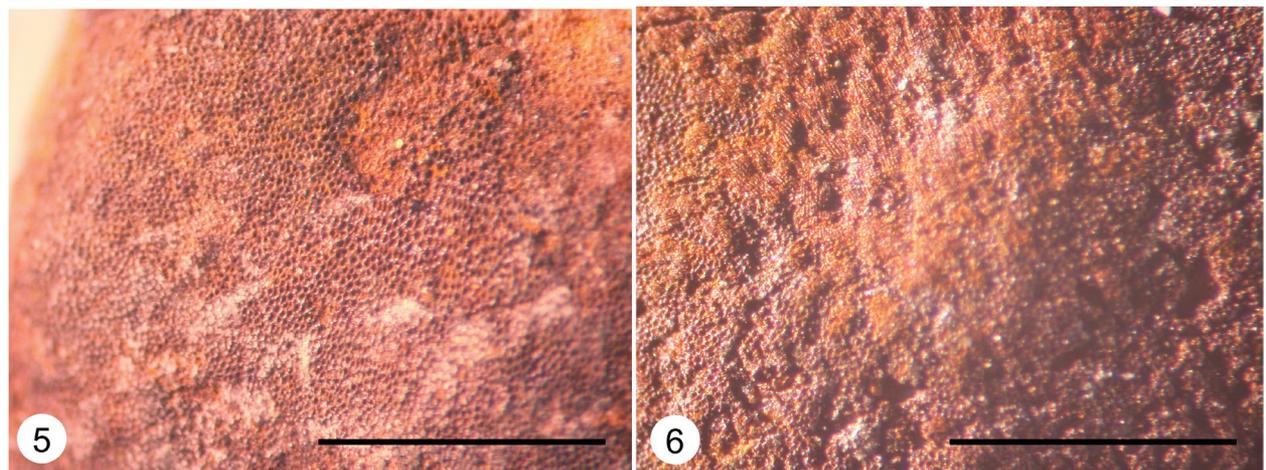
#### Family JUGLANDACEAE

#### Genus *Polyptera* Manchester et Dilcher

Pl. 2, fig. 2

Specimens. USNM 728221 (Pl. 2, fig. 2), 728222.

Remarks. Fruits of Juglandaceae have distinctive, broadly pyriform locule casts that are pointed apically, rounded basally, and basally cleaved in the position of primary septum.



**Plate 2.** Seeds and locule casts from the Newell's Nook flora. **1.** *Vitis* seed showing ventral infolds and circular dorsal chalaza, USNM 728219; **2.** *Polyptera* locule casts showing subdivisions from the primary and secondary septa, USNM 728221; **3–6.** *Libasperma potamoglossensis* seeds. Note small apical hilum and elongate raphe that almost encircles the entire seed; **3, 6.** USNM 72851; **4, 5.** USNM 728248; **5, 6.** Close up photos showing surface detail with rounded, isodiametric cells and striations. Scale bar = 1 mm

Often, the secondary septum will be marked by less prominent basal cleavage at right angles to the primary cleft. *Polyptera* is an extinct genus recognizable in more complete specimens by the configuration of its attached, multilobed, flange-like wing. Even without the preservation of the wing, however, the locule cast of *Polyptera* is easily recognized by the peculiar convolutions indicating a primary and secondary septum, and a pair of marginal lacunae (Manchester and Dilcher, 1997: figs 12, 16, 25b). Although most records of *Polyptera* are from Wyoming, a more northerly occurrence, from the lower Paleocene (age from Donovan et al., 2014) of Mexican Hat, Montana, was previously documented (Fig. 9 in Manchester and Dilcher, 1997).

#### Order CUCURBITALES

#### Family CUCURBITACEAE

#### Genus *Libasperma* gen. nov.

#### Species *Libasperma potamoglossensis* sp. nov.

Pl. 2, figs 3–6

Specimens. USNM 728248 (Pl. 2, figs 4, 5), 728251 (Pl. 2, figs 3, 6), 728247, 728250.

**Etymology.** The genus is named for the flat, pancake-like shape of its seeds. Libum (Latin = cake, pancake) + sperma (Greek = seed) = Libasperma. The epithet refers to the stratigraphic provenance in the Tongue River Member of the Fort Union Formation. Potamos (Greek = river) + glossas (Greek = tongue) = potamoglossensis.

**Diagnosis.** Seeds flattened ellipsoids, sometimes slightly pyriform, truncated at apex, rounded at base. Hilum short. Raphe marginal, encircling the seed. Surface smooth to slightly rugulate. Surface primarily consists of rounded, uniformly sized, isodiametric cells, columnar in section. A thin layer of fine striations, external to the columnar layer and oriented towards the margin, is preserved in some specimens.

**Remarks.** The presence of a small apical hilum and a raphe encircling nearly the whole perimeter of the seed suggests affinities with Cucurbitaceae (Corner, 1976). This feature is also found in other families like Annonaceae and Rhamnaceae, but the Newell's Nook seeds lack a ruminant endosperm (characteristic of

Annonaceae) and do not have wings (common in Rhamnaceae). The smooth or slightly rugulate surface with equally spaced cells is similar to some extant Cucurbitaceae. In section, one can see the columnar cells of the thin seed coat (e.g. USNM 728250). In surface view, this cell pattern is isodiametric. These may be related to Cucurbitaceae fossil leaves of *Cucurbitaciphyllum lobatum* (Knowlton) Manchester (2014) described from the Fort Union Fm., but no fruits or seeds have been found in direct association with these leaves so far.

The Newell's Nook seeds resemble *Tenuispermum*, a seed type from the Eocene Clarno Nut beds (Manchester, 1994). *Tenuispermum* also has a marginal raphe that encircles the entire seed, excluding the hilum. Unlike the Newell's Nook seeds, *Tenuispermum* has a groove within the lateral ridge that encircles the seed. These seeds also resemble fossils of *Cucurbitospermum* from the Paleocene or Eocene of England (Chandler, 1961, 1962) in their shape and smooth surface; the smooth, rounded margin is especially similar to *C. lakense* (Chandler, 1962) and *C. sheppeyense* (Chandler, 1961). *Cucurbitospermum* from the London Clay include *C. cooperi*, *C. equiaelaterale*, *C. sheppeyense*, and *C. triangulare* (Chandler, 1962). *Cucurbitospermum* from the Lower bagshot flora include *C. lakense* and *C. obliquum* (Chandler, 1962).

#### Order MYRTALES

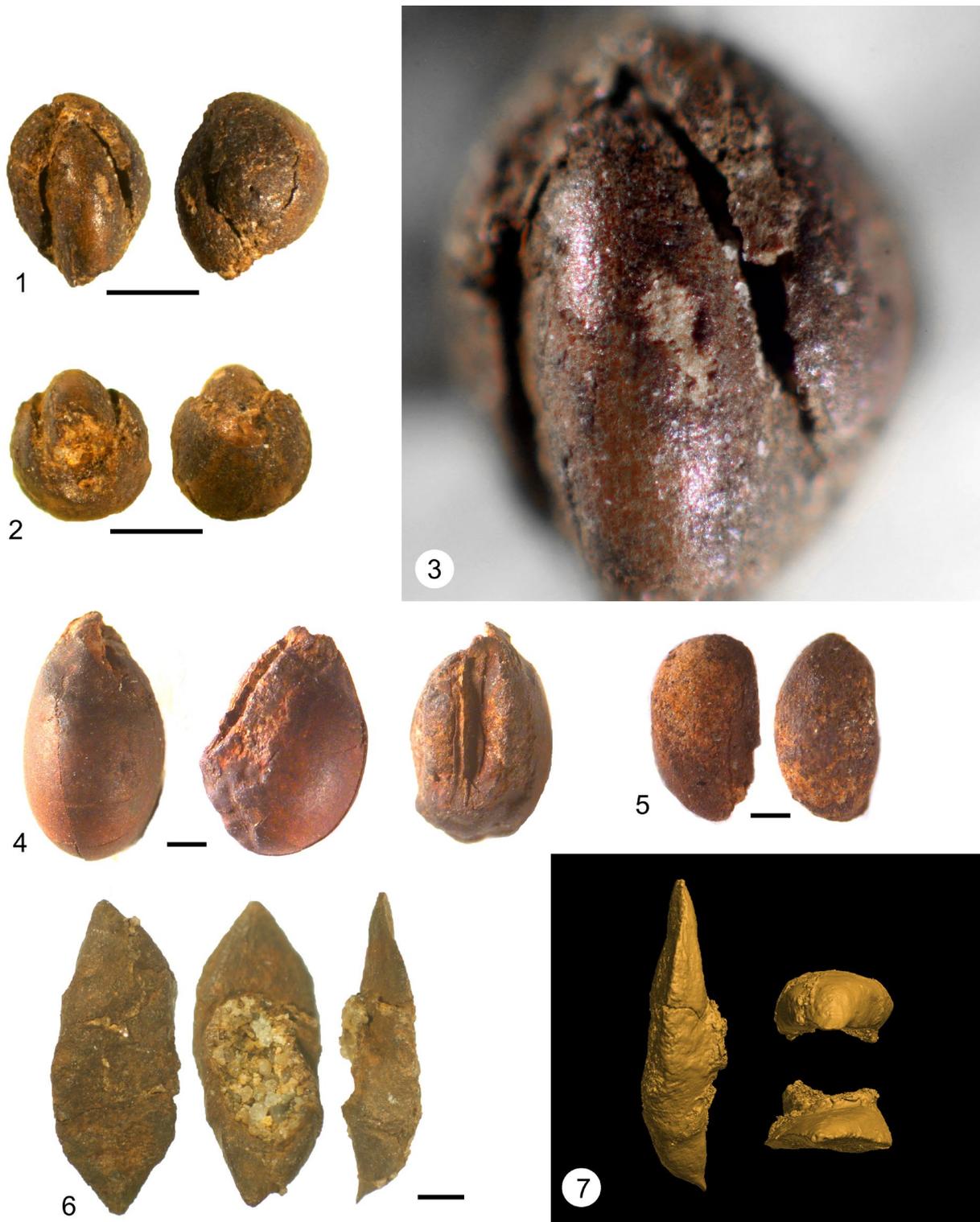
#### Family LYTHRACEAE

#### Genus *Decodon* J.F.Gmel.

Pl. 3, figs 1–3

Specimen. USNM 728246.

**Remarks.** Oval germination valves with isodiametric cell patterns occur in at least two extant genera of Lythraceae (*Decodon* and *Lawsonia*; Graham and Graham, 2014) and many extant genera (Graham, 2013). The rounded, subcircular shape of this seed conforms to the fossil genus, *Mneme* (see Dorofeev, 1977; Nikitin, 2006), but the Newell's Nook specimen can be distinguished from *Microdiptera* and *Mneme* by the lack of flattened margins that form small wings (Tiffney, 1981a; Nikitin, 2006). *Decodon* seeds lack wings and are often faceted and trihedral due to tight packing within the fruits (Tiffney, 1981a). The Newell's Nook specimen lacks wings, but it is subcircular rather than



**Plate 3.** Seeds and locule casts from the Newell's Nook flora. 1–3. *Decodon* seed, USNM 728246; 1. Front and lateral views; 2. Basal and apical views; germination valve is facing up; 3. Closeup showing elongate rectangular cell pattern on germination valve; 4. *Zanthoxylon* seeds showing elongate hilar scar, USNM 728235; 5. *Phellodendron* locule cast, USNM 728254; 6, 7. Locule casts of nyssaceous endocarp, USNM 728244; 7. Isosurface renderings showing lateral view (left), basal view (top right) and apical (bottom right) views. Scale bar = 1 mm

triangular. However, *Decodon* seeds can be highly variable in shape; the Newell's Nook specimen bears some resemblance to other *Decodon* seeds with less developed spongy tissue, like the fossil species *D. globosa* (see Tiffney, 1981a).

A note on the taxonomy of *Decodon* and *Mneme* is warranted here, as the genus *Mneme* has often been ignored. E. M. Reid transferred the type species of *Diclidocarya* to *Decodon* in a note accompanying an article by

Nikitin (1929). Contrary to the code of nomenclature (e.g. ICN, 2018; Turland et al., 2018), Reid excluded one species of *Diclidocarya* (*D. menzellii*) from synonymy with *Decodon*. The obscurity of the type *Diclidocarya*'s synonymy with *Decodon* and the persistence of *D. menzellii* left the name *Diclidocarya* in continued usage. During successive decades additional new species were incorrectly attributed to *Diclidocarya*; to resolve this problem, Eyde (1972) established the genus *Mneme* for these non-*Decodon* "*Diclidocarya*" species. Although *Mneme* was established to ease the confusion surrounding these genera, some authors still used the name *Diclidocarya* (e.g. Nitkin, 2006) contrary to the international code of botanical nomenclature.

#### Order SAPINDALES

#### Family RUTACEAE

#### Genus *Zanthoxylum* L.

Pl. 3, fig. 4

Specimen. USNM 728235.

**Remarks.** This seed is generally ellipsoid and sharply truncated by a hilar scar. Its surface is smooth, and the shape suggests the presence of a raphe that encircles the seed. Seeds of Rutaceae are characterized by an elongate, ventrally positioned hilar scar (Tiffney, 1980). In many rutaceous seeds, vasculature wraps around the seed to form a prominent raphe, large basal chalaza and small apical micropyle. The Newell's Nook seed conforms with Rutaceae in these features.

The Newell's Nook seed is within the range of sizes seen in *Zanthoxylum* (2.5–6.2 mm). The hilar scar in *Zanthoxylum* can be circular or triangular, or sometimes linear and elongate as in the Newell's Nook specimen. The surface ornamentation of *Zanthoxylum* can be intensely ridged or smooth as in our specimen. Circular hila are typical of New World taxa, while elongate hila – similar to the Newell's Nook specimen – are regular to Old World *Zanthoxylum* (Tiffney, 1980). Most Cenozoic fossils related to *Zanthoxylum* are from Europe and placed in the fossil genus *Rutaspermum*. Typically, they have a sculptured surface, unlike the Newell's Nook specimen, but a few smooth-surfaced members have been described, for example *R. chandlerae* Collinson & Gregor

from the middle Eocene of Messel, Germany. *Rutaspermum* seeds often have an elongate triangular hilum and a shape that suggests origins from a one-seeded carpel. Fossils of *Zanthoxylum* are known from Europe, Japan, China and North America (Zhu et al., 2016; Appelhans et al., 2018). The oldest fossils of *Zanthoxylum* are from the early Eocene of England, and the oldest occurrences in the New World are from the late Oligocene (Appelhans et al., 2018). The Newell's Nook material represents the oldest known occurrence of *Zanthoxylum*.

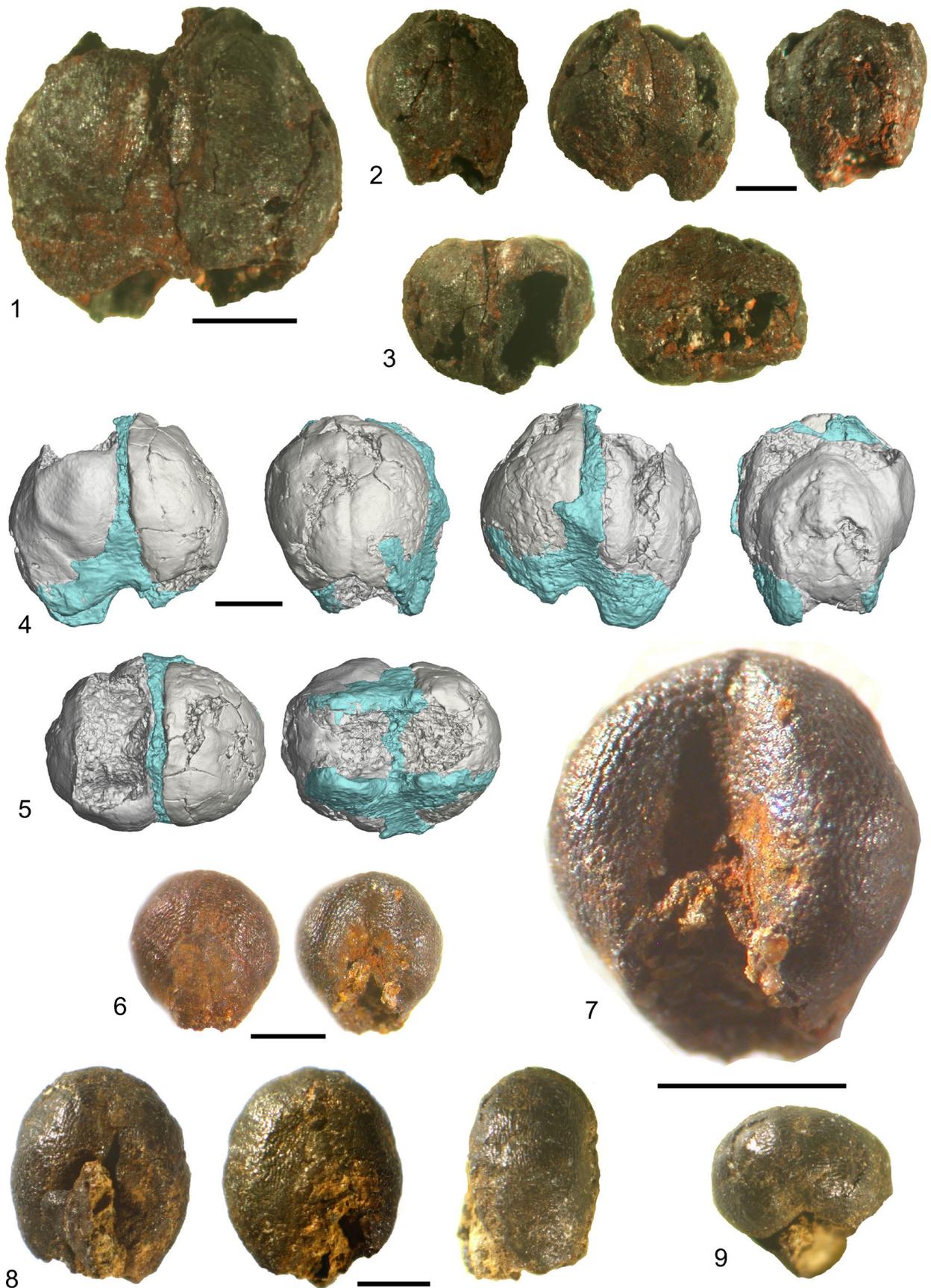
The Newell's Nook seeds also resemble a rutaceous species from the Eocene and Oligocene of Germany and Siberia referred to as *Euodia nitida* (Nikitin) Mai (alternatively known as *Carpolithus nitidus* Nikitin) from the Oligocene to Miocene of western Siberia; *C. nitidus* Nikitin was identified to extant *Euodia* by Mai (1970) but the raphe in *C. nitidus* extends halfway down the ventral face of the seed instead of the full length as in *Euodia*. *C. nitidus* seeds are inflated, likely the product of a one-seeded carpel, lacking facets or flat surfaces common in *Euodia* (Tiffney, 1981b). The inflated shape of the Newell's Nook specimen suggests it originated from a one-seeded carpel similar to *C. nitidus* and many *Rutaspermum*. *C. nitidus* seeds are smaller (1.5–1.8 mm long, and 1.2–1.3 mm wide) than our specimen (5 mm long, 3 mm wide). Outside of Rutaceae, similar seeds, inflated ellipsoids sharply truncated by elongate scars, can be found in Sapotaceae.

#### Genus *Phellodendron* Rupr.

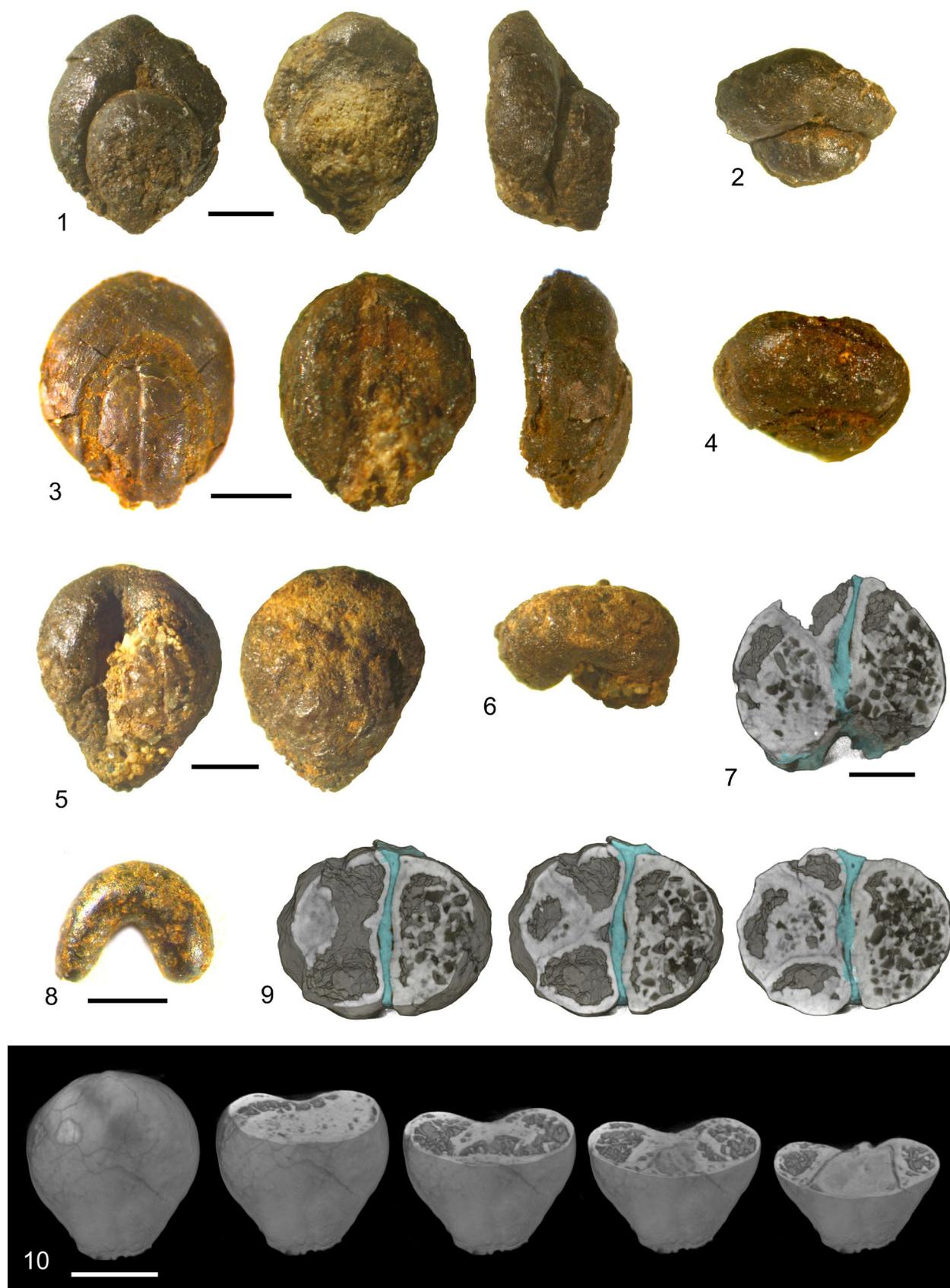
Pl. 3, fig. 5

Specimens. USNM 728254 (Pl. 3, fig. 5), 728256, 728259.

**Remarks.** These specimens likely represent the locule casts of *Phellodendron*. This is suggested by their sharp ventral face, rounded dorsal face, basal chalaza and elongate hilum. Extant *Phellodendron* seeds have a reticulate surface. The Newell's Nook fossils are smooth, lacking reticulate surface pattern, which would be expected of locule casts. *Todallia* is similar to *Phellodendron* but has more curvature to its seeds. Prior to the specimens discussed here, *Phellodendron* was thought to be in North America by the Late Eocene or Early Oligocene (Gregor, 1989).



**Figure 4.** *Honeytheca bighornensis* Huegele et Manchester sp. nov. fruits. 1–5. Holotype, USNM 728253; 1. Enlarged view showing surface detail; 2. Lateral views; 3. Apical (left) and basal (right) views; 4, 5. Isosurface renderings from CT scan. Septum is highlighted in blue; 4. Lateral views; 5. Apical (left) and basal (right) views; 6, 7. USNM 728239; 6. Lateral views; 7. Enlarged view showing surface detail; 8, 9. USNM 728240; 8. Lateral views; 9. Apical view. Note the upside-down v-shape of the disc-shaped portion of the fruit. Scale bars = 1 mm



**Figure 5.** *Honeytheca bighornensis* Huegele et Manchester sp. nov. fruits. **1, 2.** USNM 728242; **1.** Lateral views; **2.** Apical view, upside-down v-shape of the disc-shaped portion fruit; **3, 4.** USNM 728241; **3.** Lateral views; **4.** Apical view; **5, 6.** USNM 728243; **5.** Lateral views; **6.** Apical view; **7, 9.** Virtual sections from volume renderings of the holotype, USNM 728253. Septum highlighted in blue; **7.** Longitudinal section through the center of the two parted structure; **8.** Putative embryo cast related to *Honeytheca*, USNM 728236; **9.** Successive transverse sections from apex (left) to base (right); **10.** Successive transverse sections from apex (left) to base (right) of a volume rendering of USNM 728239 (also figured in Pl. 4, figs 6, 7). Scale bars = 1 mm

## Order CORNALES

## Family NYSSACEAE

## Genus indet.

Pl. 3, figs 6, 7

Specimens. USNM 728244 (Pl. 3, figs 6, 7), 728258.

Remarks. These locule casts represent Nyssaceae, which have fruits that dehisce with valves that open from the apex. The sharp keel of the locule cast corresponds to the edges of the germination valve. This suggests that the germination valve was confined to the upper half of the endocarp in these fossils. The specimens thus resemble *Nyssa* and *Camptotheca*, which have germination valves limited to the upper half of the endocarp, but *Nyssa* has broader, more strongly curved locules than these specimens and *Camptotheca* has more elongated fruits and locules. The Newell's Nook specimens are more reminiscent of the fossil genera *Amersinia* and *Eydeia*, which also have apical germination valves. The Newell's Nook specimens (at least 7.8–9.7 mm long) are in the size range for the type species of *Amersinia* from Almont, North Dakota (6.5–12 mm), but they are slightly smaller compared to some *Eydeia* (1.0–3.0 mm). The germination valves of most *Amersinia* are confined to the upper quarter of the endocarp but can rarely extend as far as the upper half of the endocarp (Huegele and Manchester, 2020). These specimens could alternatively represent other nyssaceous taxa like *Browniea* (Manchester and Hickey, 2007), or *Hironoia* (Takahashi et al., 2002), but this is unlikely since the germination valves of these genera extend down the full length of the fruit. Without preservation of the endocarp anatomy and characters like the number of ridges per locule and the number of locules per endocarp, it is difficult to determine the generic affinities of these fossils.

Order and family indet.

Genus *Honeytheca* Huegele et Manchester  
gen. nov.

Species *Honeytheca bighornensis* Huegele  
et Manchester sp. nov.

Pl. 4, figs 1–9; Pl. 5, figs 1–10

Etymology. Named for vertebrate paleontologist James G. Honey (1951–2012), who

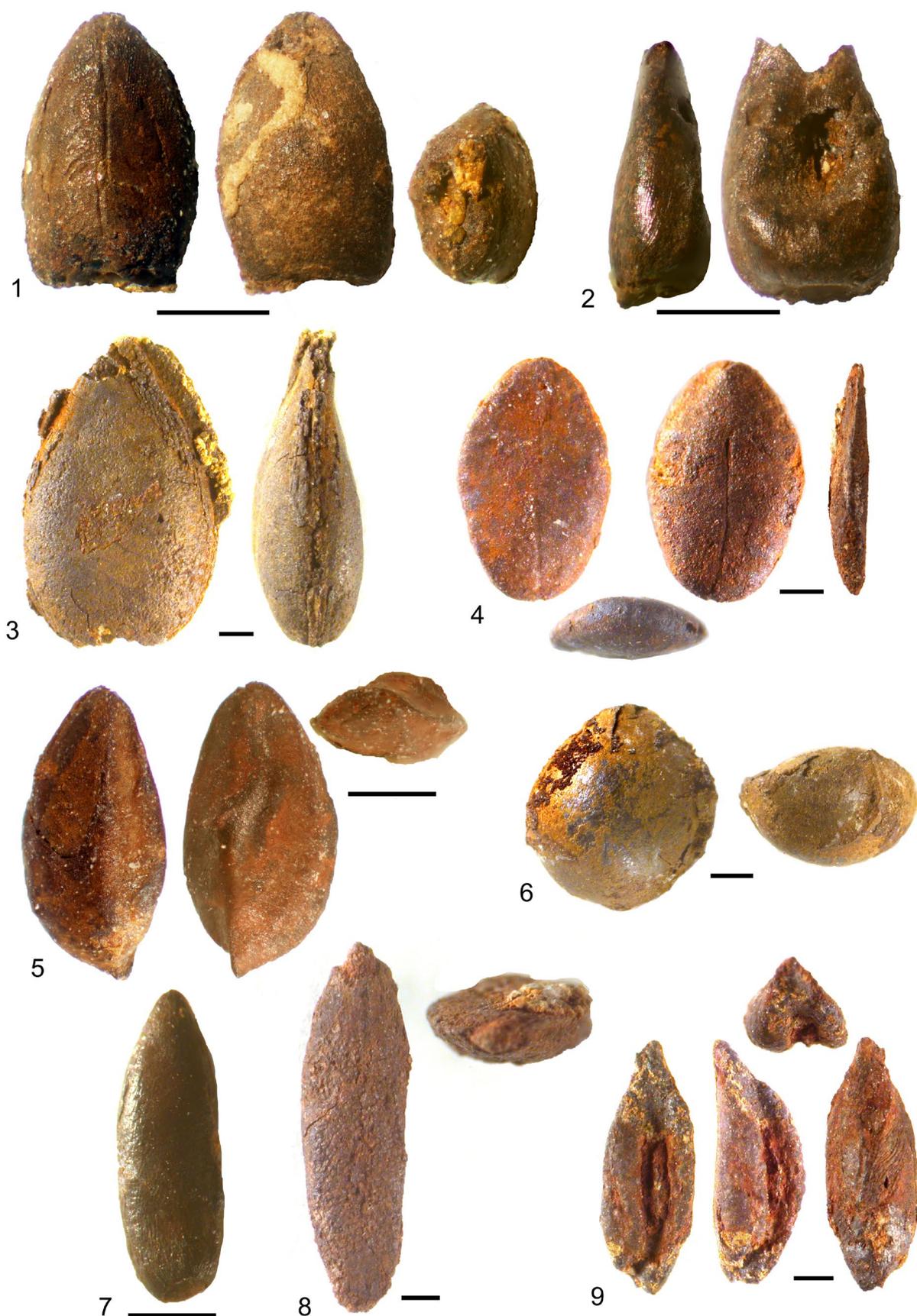
collected and loaned the Newell's Nook specimens. A biography of Dr. Honey was published by Taylor et al. (2020). The suffix, -theca (Latin = sac, bag), refers to its fruit-like nature. The species epithet refers to the type locality, which is located in the Bighorn Basin.

Holotype. USNM 728253 (Pl. 4, figs 1–5; Pl. 5, figs 7, 9).

Specimens. USNM 728239 (Pl. 4, figs 6, 7; Pl. 5, fig. 10), 728240 (Pl. 4, figs 8, 9), 728241 (Pl. 5, figs 3, 4), 728242 (Pl. 5, figs 1, 2), 728243 (Pl. 5, figs 5, 6), 728236 (Pl. 5, fig. 8).

Diagnosis. Fruit a two-parted dehiscent capsule composed of two disk-shaped halves separated by a septum. Dehiscent fruit halves each roughly disk-shaped, elliptical to sub-circular in face view, elongate in side view, bilaterally symmetrical. Apex blunt, rounded, base acute or broken with attachment scar. Outer face bears an inflated, round protrusion (lump), otherwise concave, back side convex, V-shaped in cross section. Lump apically rounded, basally truncate or pointed, extending from basal attachment 1/2–2/3 the length of the disk and bearing a medial longitudinal groove marking the plane of bisymmetry. Lump surface smooth, seed surface otherwise ornamented by uniform reticulate cell pattern.

Remarks. These disseminules, likely two-seeded fruits, are incredibly unique in shape and ornamentation. The strongly curved shape of each seed suggests campylotropy. This character is found in many families, including Theaceae, Menispermaceae, Brassicaceae, the core Caryophyllales and other families. Although most of the disseminules are preserved as isolated globular seeds (Pl. 4, figs 6–9; Pl. 5, figs 1–6, 10), one specimen (Pl. 4, figs 1–5; Pl. 5, figs 7, 9) shows two of them borne together as what seems like a bicarpellate structure. Bipartite capsules are characteristic of Brassicaceae, although we lack diagnostic features to confirm that these fossils conform to this family. In Brassicaceae, the mesocarp tissue dehisces from areas adjacent to the replum and reveal the seed. In *Honeytheca*, each of the seeds seems to be complete on both sides, i.e. they do not seem like broken or isolated valves. Isolated seeds appear broken at their base, as if the base was where the discs were detaching from the rest of the fruiting structure. The lump could represent some



**Figure 6.** Incertae sedis specimens. **1.** Incertae sedis A, USNM 728252. Lateral view and basal view. Note longitudinal groove present on one side of the endocarp; **2.** Incertae sedis B, USNM 728263. Note longitudinally oriented cells; **3.** Incertae sedis C, USNM 728237. Note layer of ribbed or wrinkled tissue; **4.** Incertae sedis D, USNM 728220. The surface consists of rounded, equally sized cells; **5.** Incertae sedis E, USNM 728261; **6.** Incertae sedis F, USNM 728216; **7.** Incertae sedis G, USNM 728227. Note circular scar at base and wavy, longitudinally aligned cells; **8.** Incertae sedis H, USNM 728258; **9.** Incertae sedis I, USNM 728234. Note general boat shape and wrinkled surface. Scale bars 1 = mm

kind of valve, but this lump is not broken nor isolated from the discs. Virtual sections from CT scan show that the lump forms a region distinct from the rest of the disseminule. Aside from our surficial comparisons with Brassicaceae, we have not found obvious affinities with extant plants and are not aware of their occurrence at other paleobotanical sites. The surface cell pattern more closely resembles that of seeds in Theaceae (e.g. Zhu et al., 2016), but Theaceae lack the bizarre lump displayed by *Honeytheca*.

#### Incertae sedis

##### Incertae sedis A

Pl. 6, fig. 1

Specimen. USNM 728252.

Remarks. This specimen is an ellipsoid, pointed at one end, sharply truncated at the other end, elliptical in cross section. One side is rounded and bears a thin, medial, longitudinal groove, the other side is flattened and lacks a medial groove. A ridge or keel encircles the lateral edges of the endocarp. The surface is mostly smooth, slightly wrinkled. A layer of tissue is preserved with cellular detail; the cells are ellipses or rounded rectangles aligned in longitudinal rows. This specimen has many similarities to *Berchemia*, a rhamnaceous genus with seeds that are sharply truncated at the base and have a medial groove running across its ventral and dorsal sides; this groove indicates the placement of a septum, which separates the two locules in these endocarps. However, the Newell's Nook specimen bears a longitudinal groove only on one side of the endocarp. The Newell's Nook specimens also lack the ribbed sculpture found in other rhamnaceous endocarps, like those of *Ziziphus* (Collinson et al., 2012).

##### Incertae sedis B

Pl. 6, fig. 2

Specimen. USNM 728263.

Remarks. This specimen is ovate, bluntly truncated at base, broken at apex and elliptical in cross section. A longitudinally elongate, elliptical depression is present on the front and back sides of the disseminule. The surface

cell structure is well preserved in this specimen; the cells are elongate, rectangular and aligned longitudinally.

##### Incertae sedis C

Pl. 6, fig. 3

Specimen. USNM 728237.

Remarks. This specimen is ovoid, pointed at apex, broken (likely rounded) at base, elliptical to lensoidal in cross section. It is 9.1 mm long. The disseminule is thinner near the apex (1.1 mm thick) and thicker (3.3 mm) at the base. Lateral edge is encircled by a rib or lip, possibly marking the position of a valve. The disseminule likely was composed of several layers; one edge of the specimen bears a fragmented layer of longitudinally ribbed tissue. No cellular details are preserved.

##### Incertae sedis D

Pl. 6, fig. 4

Specimen. USNM 728220.

Remarks. This specimen is a flattened ellipsoid, rounded at both ends. It is 5 mm long and 3 mm wide. One end is slightly more pointed than the other end; the disseminule is thicker (1.0 mm) at the blunt end and thinner (0.6 mm) at the pointed end. It has a medial groove that wraps longitudinally around the disseminule. Cellular detail is not well preserved in these specimens, but the surface seems to consist of rounded, isodiametric, equally sized cells.

##### Incertae sedis E

Pl. 6, fig. 5

Specimen. USNM 728261.

Remarks. This specimen is slightly obovate, pointed at broader end, rounded at opposite end and trigonal in cross section, ~3.1 mm long, 1–1.6 mm wide. One side of the disseminule bears a flat, elongate fracture. The shape of the fracture resembles a strap-shaped scar that is characteristic of Hamamelidoideae. Cellular detail is partially preserved; the surface is covered in rounded, regular cells that are organized in transversely aligned bands.

## Incertae sedis F

Pl. 6, fig. 6

Specimens. USNM 728215, 728216 (Pl. 6, fig. 6), 728249.

Remarks. These specimens are globose ellipsoids, 4.6–4.7 mm long, 4.0–4.1 mm wide, rounded at apex, bluntly truncated at base. The base is marked by a circular ridge. The shape of these disseminules and the morphology of the circular ridge are reminiscent of fagalean nuts, which have a circular scar marking the attachment of the cupule. The surface is smooth, bearing no ridges, similar to extant *Corylus*, which has vascular bundles inside the nut and therefore do not form external ridges. However, there are no impressions at the site of cupule attachment indicating where the vascular bundles should be. The specimen USNM 728215 is partly fractured revealing a resistant layer, possibly a seed coat, preserved in limonite, uniformly about 0.3 mm thick. USNM 728216 has some cellular detail preserved; the cells are rounded, almost circular, and regular in size. These disseminules are similar to specimens described as *Corylus* nuts by Roland Brown (Brown, 1962; see comments in Manchester, 2014).

## Incertae sedis G

Pl. 6, fig. 7

Specimen. USNM 728227.

Remarks. This disseminule is elongate, ovoid, rounded at base, pointed at apex and elliptic in transverse section. The base is marked by a circular scar. The surface, aside from the base, is covered by roughly rectangular cells aligned in wavy, longitudinally aligned rows. The shape of these seeds is reminiscent of Hamamelidaceae, but the circular scar at its base is not characteristic for the family.

## Incertae sedis H

Pl. 6, fig. 8

Specimen. USNM 728258.

Remarks. This disseminule is elongate, ellipsoidal, rounded trigonal in cross section, rounded at base and apex. One end thins and is slightly broken. Cellular detail is not preserved.

## Incertae sedis I

Pl. 6, fig. 9

Specimen. USNM 728234.

Remarks. This specimen is ovate, acutely pointed at apex, truncate at base, c-shaped in cross section and bears a medial longitudinal groove. In the center of this specimen, the groove has a slight protrusion. Surface is mostly smooth; faint horizontal wrinkles are present on one side. This specimen resembles the boat-shaped endocarps of mastixioids (for example, compare with *Mastixicarpum*, fig. 4 in Huegele and Manchester, 2020), but there are not enough characters preserved to confirm such affinities. Cellular surface details are not well preserved.

## Incertae sedis J

Specimen. USNM 728262.

Remarks. This specimen is boat shaped – elliptical in face view and broadly U-shaped in cross section. Both ends of the specimen are broken. Surface smooth.

## Incertae sedis K

Specimen. USNM 728260.

Remarks. This specimen is globose and fractured; only half of the disseminule is preserved. One end seems to have a circular mark, possibly representing the chalaza, but it is unclear if this represents an anatomical feature or diagenesis. No cellular detail is preserved.

## DISCUSSION

COMPARISON  
WITH OTHER PALEOCENE FLORAS

The Newell's Nook flora serves as another rare example of a Paleocene carpoflora in North America. In total, we have found 26 types of disseminules, of which 14 can be identified to modern families, including Characeae, Taxaceae, Menispermaceae, Sabiaceae, Hamamelidaceae, Cercidiphyllaceae, Vitaceae, Juglandaceae, Cucurbitaceae, Lythraceae, Rutaceae and Nyssaceae. The flora has similarities to both older and younger Paleocene carpofloras (Table 1), with shared families

including Taxaceae, Menispermaceae, Sabiaceae, Hamamelidaceae, Cercidiphyllaceae, Vitaceae and Juglandaceae. *Kingsboroughia rostellata* and cornalean taxa are shared components among these floras and reinforce the idea that these mid-latitude floras could support subtropical taxa. Newell's Nook and Littleton lack the ginkgoaceous, platanaceous, betulaceous and icacinaceous components that Almont and Sand Draw floras share. The fruits and seeds from Newell's Nook augment those from other sites in the Tongue River Member in southeastern Montana (reviewed, Manchester, 2014). These sites include cornalean taxa (*Amersinia*, *Brownia* and *Davidia*), as well as Trochodendraceae (*Nordensioeldia*), Cannabaceae (*Celtis*) and Sapindaceae (*Aesculus*).

Fruits and seeds of the Newell's Nook flora are moderate in size, not exceeding 10 mm in length, except in *Jenkinsella*, which can have fruits roughly 16 mm long. *Jenkinsella* produces the largest fruits in this flora, but it is known to disperse small, winged seeds only a few millimeters long (Crane and DuVal, 2013; Golovneva and Alekseev, 2017). Aside from *Jenkinsella* fruits, the largest disseminule in the assemblage is *Incertainia* (9.3 mm long). The smallest fruits include *Palaeoluna* and *Honeytheca*, which are ~2–3 mm in length, but the even smaller (0.4–0.7 mm in diameter) oospores of Characeae are also represented in this assemblage. Most of the fruits and seeds are in the range of 4–7 mm in length. The range of volume for fruits and seeds was in the range of ~ 4–226 mm<sup>3</sup>, but the majority of fruits and seeds excluding *Jenkinsella* had a volume of less than 50 mm<sup>3</sup>. These values complement the trends of increasing fruit and seed size from the Cretaceous into the late Eocene observed by Eriksson et al. (2000) and Tiffney (1984).

Characeous oospores are a unique element compared to other Paleocene carpoifloras and may represent the community living in the pond of deposition where the other, allochthonous elements of the flora were deposited and later fossilized. Another possible explanation could be that the oospores were transported and left behind by birds. Modern Characeae are known to be grazed by waterbirds (van den Berg, 1998b) and viable oospores have been found to survive the intestinal track of a variety of birds (Proctor and Malone, 1965), suggesting that birds may serve as a mean for Characeae dispersal. Characeae, both extant

and extinct, have been documented to grow in a wide range of salinities, from freshwater to hypersaline (Soulié-Märsche and García, 2015; Winter et al., 1996). As such, it is difficult to make inferences as to the salinity of this environment without further taxonomic resolution. The association with light and nutrient concentration seems clearer; many Characeae prefer shallow, clear waters that do not have an overabundance of nutrients (van den Berg et al., 1998a, b; Bicudo and Bueno, 2013). Assuming that the preferences for the Newell's Nook Characeae were similar to that of extant Characeae, they may indicate that the nearby water bodies were clear, possibly shallow, and unlikely to be hypereutrophic.

#### EXOTIC ELEMENTS AND EXTINCT TAXA

Most of the Newell's Nook flora appears to be exotic elements that are not found in present-day Montana. Of the plant taxa identified to family level here, only five occur in Montana today (i.e. Taxaceae, Menispermaceae, Vitaceae, Cucurbitaceae, and Lythraceae). Sabiaceae, Hamamelidaceae, Cercidiphyllaceae, Juglandaceae, Rutaceae and Nyssaceae are not found in present-day Montana; many of these elements prefer warmer, wetter conditions than are present in the region today. For example, modern Nyssaceae are well-adapted to wetland environments, although they can inhabit a wide range of temperatures, from tropical to temperate (Eyde, 1997), and *Kingsboroughia* prefers tropical to subtropical environments (Van Beusekom, 1971). Collectively, the assemblage suggests that the environment was warmer and wetter than it is today.

Among the taxa identified to genus level (11 out of the 26 morphotypes described here), roughly half of them can be placed in extant genera. These include cf. *Taxus*, *Kingsboroughia*, *Vitis*, *Decodon*, *Zanthoxylon* and *Phellodendron*. Those not assigned to modern genera are either known to be extinct (e.g. *Jenkinsella*) or do not provide sufficient features to distinguish among multiple genera with disseminules of similar morphology.

#### SIGNIFICANCE OF LIBASPERMA FOR THE CUCURBITACEAE FOSSIL RECORD

The fossil record of Cucurbitaceae is sparse, which makes the fossils of *Libasperma* all the more significant as one of the earliest records

of the family. The oldest cucurbitaceous fossils include seeds of *Cucurbitospermum* from the upper Paleocene or lower Eocene London Clay flora and the likely Eocene Lower Bagshot flora of Southern England (Chandler, 1961, 1962; Collinson et al., 1993), the leaves of *Cucurbitaciphyllum lobatum* (Knowlton) Manchester from the Fort Union Fm. (Manchester, 2014), and possibly the woods of *Tetrameleoxyton* from the Deccan Traps (Maastrichtian or early Paleocene; but this more likely may represent fossil relatives of *Tetrameles*, see Zhang et al., 2006). Younger seed records include several fossil species of *Cucurbitospermum* and *Lagenaria* from the Miocene of Rusinga Island in Lake Victoria, Kenya (Collinson et al., 2009) and *Bryonia*-like seeds known from the Miocene of Tambov, western Siberia (Dorofeev, 1963, 1988; Renner and Shaefer, 2016). *Libasperma* may represent one of the oldest known records of Cucurbitaceae seeds.

It is thought that Cucurbitaceae had an Asian origin and then later underwent multiple transoceanic long-distance dispersal events to the New World, Africa and Australia (Schaefer et al., 2009; Renner and Schaefer, 2016). The Newell's Nook record shows that they must have been in the New World by the early to mid-Paleocene. It is also thought that North American Cucurbitaceae originated from Central or South American lineages (Schaefer et al., 2009). The Newell's Nook locality seems far from hypothetical origins in Central or South America.

#### FOOD FOR MAMMALS AND BIRDS

The Newell's Nook flora is a rare example where well-preserved fossils of both animals and plants co-occur. The mammalian fauna of Newell's Nook includes at least three genera of multituberculates (*Ptilodus*, *Anconodon* and *Neoplagiaulax*), three genera of Marsupials (cf. *Peradectes*, *Acmeodon* and *Propalaeosinopa*), a few primates (cf. *Palaechthon*, *Nannodectes*, *Paromomys* or *Ignacius*, and *Picrodus*) and several condylarths (cf. *Tricentes*, *Ectocion*, *Litomylus*, *Haplaletes* and *Anisonchus* (Robinson and Honey, 1987)). As suggested by the fruits and seeds documented here, the vegetation which supported the fauna included a variety of trees (e.g. Taxaceae, *Kingsboroughia*, *Polyptera*) shrubs or woody herbs (e.g. *Decodon*) and possibly herbs and vines (e.g. *Libasperma*, *Honeytheca*). The vast majority of Cucurbitaceae

are herbs or climbing vines (there is one arborescent genus, *Dendrosicyos*; see Olson, 2003), suggesting that cucurbitaceous fossils here represent an herbaceous or vining species. Another candidate for a vining species is *Incertae sedis* A, which closely resembles *Berchemia*, a genus with some extant species that are climbers. If the affinities of *Honeytheca* with Brassicaceae are correct, it may serve as evidence for herbaceous taxa at this locality.

Among the disseminules known from Newell's Nook, several had fleshy coverings, judging from their extant relatives (e.g. *Taxus*, *Diploporus*, Menispermaceae, *Kingsboroughia* and *Vitaceae*). These were likely attractive to birds and mammals that aided in dispersal. Others, like *Polyptera*, had small nuts that could have been eaten and dispersed by mammals, although they also possessed elaborated bracts suitable for wind dispersal. Extant Characeae are known to be dispersed by waterfowl and may represent a large percentage of waterfowl diet (Bonis and Grillas, 2002; also see Rip et al., 2006). However, no avian fossils are known from the Newell's Nook locality. We did not recover any direct evidence of animal interaction; the fossils lack obvious bite marks, which are known to preserve in some other carpofloras (e.g. Huegele and Manchester, 2019). Taken collectively with other fruits from the Tongue River Member, these fruits indicate a range of food choices for the mid-Paleocene fauna and show a range of both abiotic and biotic dispersal mechanisms.

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