AN EARLY PALEOCENE CARPOFLORA FROM THE DENVER BASIN OF COLORADO, USA, AND ITS IMPLICATIONS FOR PLANT-ANIMAL INTERACTIONS AND FRUIT SIZE EVOLUTION

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Premise of research. Fossil fruit and seed floras are valuable because of the wealth of taxonomic characters that they can provide, but they are rare in the Cenozoic of North America. Here, we document a fossil fruit and seed flora from the Paleocene Denver Formation of the Denver Basin, Littleton, Colorado, representing the first account of an early Paleocene carpoflora in North America. This locality has previously yielded a rich and well-studied therian and sauropsid fauna confirming a Puercan age. In conjunction with these vertebrate records, the Littleton flora serves as an ecological snapshot of a transitional time in both angiosperm and vertebrate lineages following the K-T mass extinction event.

Methodology. Disseminules were studied with reflected light and X-ray micro-computed tomography.

Pivotal results. The flora contains at least 15 different morphotypes, including four members of the Cornales (Amersinia littletonensis sp. n., Langtonia parva sp. n., Mastixicarpum hoodii sp. n., and Portnallia alexanderi sp. n.). The occurrence of Kingsboroughia rostellata (Lesquereux) comb. n., a close relative of Meliosma (Sabiaceae), is among the earliest records for this genus in North America. Although the morphology of the Littleton fruits and seeds is consistent with animal dispersal and in agreement with dietary preferences suggested by mammalian dentition, wear from predation is not evident in any of these specimens.

Conclusions. The fruits and seeds reveal components of the early Paleocene Denver Basin flora that were not known from prior investigations of leaf assemblages. However, modern-day relatives of the Littleton taxa may occupy environments similar to those inferred for other Paleocene floras in the Denver Basin. Although the Littleton disseminules were found to have larger fruits and a wider range of sizes than other Paleocene floras, they fit into previously recognized trends of increasing seed size from the late Cretaceous through the early Tertiary.

Keywords: Denver Formation, Paleogene, paleobotany, fruit and seed size, Kingsboroughia, Mastixicarpum, Portnallia.

Introduction

The Paleocene flora of western North America is best known from fossil leaves and pollen, but carpo floras from that time are uncommon. Fruits and seeds—because of their distinctive characters—can provide greater systematic resolution than leaf remains and have facilitated the recognition of some important components in Paleocene floras, including Cyclocarya Ilijinsk, Polyptera Manchester & Dilcher, Davida Baill., Amersinia Manchester, Crane, & Golovneva, Aesculus L., Sloanea L., and Nordenskjoldia Heer (Manchester and Dilcher 1982, 1997; Manchester et al. 1991, 1999; Manchester 2001, 2002; Manchester and Kvaček 2009). However, most of these fruits were found as rare specimens in siltstone and shale sediments dominated by leaf fossils; few fossil floras wherein carpological material is the primary component exist in North America. Some assemblages with abundant fruit remains include those from the late Paleocene (e.g., Almont, North Dakota: Crane et al. 1990; Sand Draw, Wyoming: Tiffney and Manchester 2019), but early Paleocene carpo floras are rare. Here we present a newly recognized fruit and seed flora from the early Paleocene of Littleton, Colorado, introducing the first description of an early Paleocene carpoflora from North America.

The Littleton biota is known for its well-studied diversity of vertebrate fossils, including turtles, squamates, crocodylians, amphibians, gars, prototherians (egg-laying mammals), metatherians (marsupial mammal relatives), proteuthers (ancient placental mammals), and eutherians (true placental mammals), referred to as the Alexander fauna (Middleton 1982; Dewar 2003; Eberle 2003; Middleton and Dewar 2004). Condylarth (ancient hooved mammals; Dewar 2003), scincomorphs (Sullivan and Lucas 1996), and arctocyonids (Eberle 2003) are some of the noteworthy elements of this assemblage. The Alexander
fauna has been said to represent “arguably the most diverse palaeo-biofacies known from the early Paleocene in North America,” with more than 21 mammal species described along with other vertebrates (Middleton and Dewar 2004, p. 60). In his initial description of the fauna, Middleton (1982) mentioned the presence of fossil plants at the Alexander locality but only generally as “wood, leaves, and seeds” of unnamed taxa.

This study represents the first detailed account of the floristic diversity of this locality. Studying fruit and seed material may allow us not only to uncover the taxonomic diversity of extinct floras but also to better understand past plant-animal interactions (Tiffney 2004), presenting a rare opportunity to reconstruct a more complete picture of Paleocene life. Here we describe and illustrate 15 morphotypes from semipersimeralized fruits and seeds. These include five new species, *Amersinia littletonensis* sp. n., *Langtonia parva* sp. n., *Mastixicarpum hooidii* sp. n., *Portaulia alexanderi* sp. n., and *Kingsboroughia rostellata* (Lesquer­euix) comb. n. We consider the systematic and biogeographic implications of these taxa as well as their ecological significance. The average and range of disseminule size for this flora are also considered in the context of previously recognized changes in seed size through Cretaceous and Cenozoic time. Last, we interpret the possible interactions between these represented fruit and seed taxa and the co-occurring Littleton fauna.

**Material and Methods**

Our study is based on a collection of 167 specimens made by Glen and Donna Hood that was donated to the Denver Museum of Nature and Science (DMNH) and curated under the locality designation DMNH 8726 and on an additional 46 specimens that were collected from the same site in 2017 and 2019 by S. Manchester and I. B. Huegele and deposited at the Florida Museum of Natural History, Gainesville, Florida, under the locality designation UF 19431. Another collection was made by a local resident, Carl Alexander, who donated hundreds of specimens to the Museum of Natural History at the University of Colorado, Boulder (CU). Most of these specimens are on long-term loan to Dr. Margaret Collinson in London and were not considered in this study.

Vertebrate biostratigraphic correlations of the co-occurring Alexander fauna (recorded under the locality UCM 72267) place the site in the Pu1 and earliest Pu2 zones of the Puercan Land Mammal Stage (Eberle 2003), Located in the D1 unit of the Denver Formation (~65.5–63.79 Ma; Johnson et al. 2003), this locality has been dated by paleomagnetic analyses to be slightly less than 64 million years old (Middleton and Dewar 2004). The beginning of the Puercan is marked by the presence of *Protoungulatum* Sloan & Van Valen, while its ending is characterized by the appearance of Periptychus Cope (Eberle 2003). Upon returning to the site in 2017 and 2019, we were limited in our collecting to the remaining vacant lots adjacent to recently constructed buildings.

The fruits and seeds are preserved mainly as three-dimensional silicic molds and casts freed from the surrounding soft matrix by erosion. They were picked up by hand from the soil surface over an area estimated to be about 5 ha, with its center point at lat. 39°34.502N, long. 105°00.176W. This method of collection was likely biased against the recovery of very small (<1.3-mm) disseminules. Although cellular details are not preserved, the casts show differential preservation of former cavities versus wall layers, and X-ray tomography has revealed areas of secondary crystallization within some specimens. In some cases, it is difficult to distinguish between original tissue layers of the fruit and zones of secondary recrystallization. After segregating the specimens into distinct morphotypes, we selected the specimens of each morphotype that were preserved with the greatest amount of original detail for illustration. In a few instances, specimens were sectioned physically with a paper-thin diamond blade using a Microslice 2 annular saw, and resulting sections were photographed by reflected light using a Zeiss Photomacroskop M-400 equipped with a Canon SLR camera.

The specimens were documented using standard reflected-light photography and imagery from micro-computed tomography (μCT). The application of μCT allowed us to create accurate surface visualizations and digital sections of the disseminules, facilitating a view of their internal morphology from a variety of different orientations without being destructive to the specimens. Specimens were scanned at the University of Florida College of Engineering Nanoscale Research Facility (NRF) with a GE Phoenix xTome|x m240 CT scanner using a tungsten reflection target at 80 kV and 580–600 μA, producing two scans with 1500–1800 images at voxel sizes of ca. 53.08 μm. Modern *Kingsboroughia alba* (Schldt.) Liebm. fruits were scanned using the same equipment but at 48 kV and 400 μA with 2200 images at a voxel size of 19.81613 μm. Scans were processed in Avizo (ver. 9.0.0; FEI Visualization Sciences Group, Hillsboro, OR) and VGStudio Max (ver. 3.1; Volume Graphics, Charlotte, NC). Although Avizo was used to initially explore scans, the illustrations figured in this article were generated from VGStudio Max. Original TIFF stacks, animations, and other imagery produced from this material can be found at http://www.morphosource.org/Detail/ProjectDetail/Show/project_id/846.

Disseminule size was assessed for the Littleton specimens in the manner prescribed by Tiffney (1984), wherein the length, width, and thickness of each specimen were multiplied to provide an estimated volume. In cases of slightly damaged or compacted fruits and seeds, an estimate of the depth was made based on the width multiplied by 0.66 (Tiffney 1984), while estimates of length were based on the average length for whole specimens of that type. Among the 167 specimens, 14 were poorly preserved or fragmented beyond meaningful interpretation, while another 23 could be measured for length, width, or depth but could not be used to estimate volume.

**Results**

**Systematics**

**Order**—Proteales Juss. ex Bercht. & J.Presl

**Family**—Sabiaceae Blume

**Subfamily**—Meliosmoideae Mast.

**Genus**—Kingsboroughia Liebm.

**Species**—Kingsboroughia rostellata (Lesquer­euix) Huegele & Manchester comb. n. (Fig. 1)
Fig. 1  *Kingsboroughia rostellata* (Lesquereux) Huegele & Manchester comb. n. and extant *K. alba* endocarps. A–E, *Kingsboroughia rostellata*. A, B, DMNH EPI.49279. A, Isosurface rendering of (from left to right) ventral, lateral, dorsal, and apical views, showing pronounced dorsal keel and ventral pore. B, Transverse section through center of endocarp, showing locule (light gray) and surrounding thick endocarp wall, volume rendering. C, DMNH EPI.49283, isosurface rendering in ventral, lateral, and dorsal views. D, DMNH EPI.49322, a locule cast; isosurface rendering in ventral, lateral, and basal views. E, DMNH EPI.49280, a larger specimen; isosurface rendering in ventral, lateral, basal, and apical views. F, G, Modern *K. alba*. F1844391, Veracruz, Mexico. F, Volume rendering, ventral view. G, Transverse section showing thick endocarp wall, seed, ventral pore, and plug. Scale bars = 1.0 mm; scale bar for A also applies to C–E. Scale bar for B also applies to F and G.
Basionym. Carpites rosettatus Lesquereux (1878. The Tertiary Flora, Report of the USGS Geological Survey of the Territories, p. 303, pl. 60, figs. 12, 13).

Synonymy. Meliosma rosettata (Lesquereux) Crane, Manchester, & Dilcher (1990. Fieldiana Geology 1418, p. 32, fig. 21A, 21B, 21D–F).

Type locality. Golden, Colorado.

Specimens examined. DMNH EPL49278, 49279 (fig. 1A, 1B), 49280 (fig. 1E), 49281, 49282, 49283 (fig. 1C), 49318, 49319, 49320, 49321, 49322 (fig. 1D), 49323, 49324, 49325, 49326, 49327, 49328, 49329, 49330, 49360, 49427. UF 19431-62631, 19431-81894.

Description. Endocarps subglobose, oboviform, 4.5–8 mm long, 4.1–8 mm wide, 3.5–6.4 mm deep, single seeded, bearing a pronounced dorsal keel in plane of bisymmetry extending longitudinally and curving ventrally to a rounded-triangular ventral pore (ca. 1.6–2.3 mm long and 1.2–2.2 mm at its widest). Surface smooth; broad ridges sometimes radiate around ventral scar. Wall ca. 0.2–0.7 mm thick.

Comments. These specimens are easily recognized as either Meliosma Blume or Kingsboroughia by their prominent ventral scar and dorsal keel (van Beusekom 1971). Kingsboroughia, formerly a section within Meliosma, was recently resurrected as a genus on the basis of molecular phylogenetic analyses (Yang et al. 2018) consistent with distinctions in both floral and vegetative characters (van Beusekom 1971). It includes a single extant species, K. alba, from southern China and Mexico. The endocarps from the Littleton flora closely follow the shape of the included seed, have a smooth surface, and lack a marginal funicular canal and a ventral protrusion (formed by the indurated ventral tip of the seed). These features indicate affinities with Kingsboroughia rather than with Meliosma (van Beusekom 1971; Yang et al. 2018). Kingsboroughia alba (fig. 1F, 1G) closely corresponds to the Littleton specimens in endocarp shape, wall thickness, and size, further supporting our placement of the Littleton fruits into Kingsboroughia. Endocarps of this morphology were first recognized from the Paleocene of the Denver Basin in Golden, Colorado, about 25 km north-northwest of Littleton, by Lesquereux (1878), who described them as C. rosettatus. Subsequently, Crane et al. (1990) described better-preserved silicified specimens from the late Paleocene Sentinel Butte Formation of North Dakota and assigned them to K. rosettata. Given the new systematic distinction of Kingsboroughia, we assign these North American specimens to K. rosettata. Other fossil endocarp species that likely represent Kingsboroughia include M. cantiensis Reid & Chandler and M. jenkinsii Reid & Chandler from the early Eocene of southern England (Reid and Chandler 1933); M. gomnensis Mai from the upper Paleocene of Gonna, Sangerhausen, Germany (Mai 1987); and M. berryi Huegele & Manchester from the late Eocene of Trinity, East Texas (Huegele and Manchester 2019).

Order—Cornales Link.

Genus—Amersinia Manchester, Crane, & Golovneva

Species—Amersinia littletonensis Huegele & Manchester sp. n. (Fig. 2)

Etymology. Named after its type locality in the town of Littleton, Colorado.

Holotype. DMNH EPL49347 (fig. 2A–2C).

Type locality. Littleton, Colorado. DMNH 8726, UF 19431.

Other specimens examined. DMNH EPL49284 (fig. 2O, 2P), 49285 (fig. 2H–2I), 49286, 49287, 49288, 49296 (fig. 2L, 2S), 49297 (fig. 2K, 2Q, 2R), 49302 (fig. 2M, 2N), 49306 (fig. 2F, 2G), 49307, 49308, 49309, 49310, 49311, 49315, 49343, 49344, 49345, 49346 (fig. 2D, 2E), 49348, 49352, 49364, 49368, 49369 (fig. 2V), 49371, 49372, 49373, 49377, 49378, 49380, 49381, 49382, 49383 (fig. 2T, 2U), 49384, 49388, 49392, 49393, 49397, 49399, 49401, 49402, 49404, 49412, 49413, 49414, 49417, 49426.

Diagnosis. Endocarp ovoid to fusiform, 2.9–12 mm long and 1.9–6.3 mm wide, length-to-width ratio 1.2–3.1, pointed basally, rounded or pointed apically with an apical stylar protrusion and a weak subapical collar (formed by an epigenous perianth), tetralocular, 1–4 ridges per germination valve. Ovate to lensoidal in longitudinal section, square or rectangular in elliptical in transverse section. Germination valve one per locule, opening apically, hinging basally from, near, or just below apical upper half of endocarp. Locules trapezoidal to subtriangular in transverse section. Wall uniformly thick, ca. 0.2–1.0 mm (average, 0.6 mm).

Comments. On the basis of locule morphology and the lack of a central vascular channel, these specimens resemble fruits of the Cornales, specifically the nyssoids, which have germination valves confined to the apical half of their endocarps. While they differ from many nyssoids, such as Nyssa Gronov. ex L., Camptotheca Decne., Browninia Manchester & Hickey, and Davidia (see Manchester et al. 1999; Atkinson et al. 2017), in transverse outline, endocarp shape, and locule number, these Littleton specimens resemble the extinct genera Amersinia (Manchester et al. 1999), Hironoia Takahashi, Crane, & Manchester (Takahashi et al. 2002), and Eydeia Stockey, Nishida, & Atkinson (Stockey et al. 2016) in these same traits (see table 1). Eydeia is characterized by ridged germination valves and vascular bundles within its septa (Atkinson et al. 2019). Although vascular bundles have not been obviously preserved in the Littleton fruits, the locule shape and appearance in transverse section and the presence of one to three ridges per germination valve suggest affinities with Eydeia. The length of Eydeia germination valves can vary, but they are usually elongate in all species except Eydeia jerseyensis (Atkinson et al. 2019). By contrast, Amersinia has shorter germination valves (occurring in the upper quarter of the endocarp) compared with those in the Littleton fruits (which occur in the upper half or just below it). The large variation in the Littleton fruits’ sizes (ca. 2.9–12 mm) may be attributed to different levels of maturity. This size range compares well with Amersinia (ca. 6.5–12 mm long; Manchester et al. 1999), but the Littleton species is mostly tetralocular, while previously recognized occurrences of Amersinia are typically trilocular and only rarely tetralocular. The septa separating the locules of Eydeia and Amersinia endocarps extend beyond the valves to produce longitudinal ribs, a feature also seen in the Littleton endocarps. Hironoia can be tetra- or trilocular, but its endocarps are nearly half the size of the Littleton fruits, and its germination valves extend down the whole endocarp length. Overall, on the basis of locule number, appearance in longitudinal and transverse sections, the presence of an apical collar, apical germination valves, and overall endocarp shape, these fruits conform best with the generic concept of Amersinia.
Fig. 2  *Amersinia littletonensis* Huegele & Manchester sp. n. endocarps. A–C, Holotype of *A. littletonensis*, DMNH EPL49347. A, Isosurface rendering, lateral views. Third view from left shows detached apical germination valve. B, Isosurface rendering, apical (top) and basal (bottom) views. C, Successive transverse sections from (from left to right) apex to base, showing septa (dark gray) delimiting four locules (light gray), volume rendering. D, E, DMNH EPL49346 isosurface renderings. D, Lateral views; note extent of calyx almost to the apex. E, Apical view. F, G, DMNH EPL49306 isosurface renderings. F, Apical view. G, Lateral views. H–J, DMNH EPL49285. H, Isosurface rendering, lateral views. I, Isosurface rendering, apical (top) and basal (bottom) views. J, Successive transverse sections from (from left to right) apex to base, showing four locules (light gray). K, Q, R, DMNH EPL49297. K, Successive transverse sections from (from left to right) apex to base. L, S, DMNH EPL49296. L, Transverse section through broken specimen showing fracture (indicated by arrows) that possibly outlines the germination valve. M, N, DMNH EPL49302 isosurface rendering. M, Lateral views, showing multiple longitudinal ridges. N, Apical (top) and basal (bottom) views. O, P, DMNH EPL49284. O, Isosurface rendering, lateral views. P, Transverse section showing four locules (light gray), volume rendering. Q, Isosurface rendering, lateral views. R, Isosurface rendering, apical (top) and basal (bottom) views. S, Isosurface rendering, lateral views, showing broken face and exposed locule. T, U, DMNH EPL49383 isosurface renderings, showing elongate germination valve extending slightly below apical half of the endocarp. T, Oblique view. U, Lateral views. V, DMNH EPL49369 isosurface rendering. Endocarp possibly dehisced or broken. Scale bars = 1.0 mm; scale bar for A also applies to B–J, M–P, and T–V. Scale bar for Q also applies to K, L, R, and S.
Amersinia obtrullata was originally described from infructescences as well as isolated fruits from the Paleocene of northeast China, northeast Russia, Alberta, Montana, Wyoming, and North Dakota (Manchester et al. 1999). The Littleton Amersinia marks a new southern extent for this genus.

**Family**—Mastixiaceae Calestani

**Genus**—Langtonia Reid & Chandler

**Species**—Langtonia parva Huegele & Manchester sp. n. (Figs. 4, 9F)

*Etymology.* Named with the Latin adjective *parva* for the small size of its endocarps.

*Holotype.* DMNH EPL49439 (fig. 3A, 3B).

*Type locality.* Littleton, Colorado, DMNH 8726, UF 19431.

*Other specimens examined.* DMNH EPL49435 (fig. 3C–3F).

*Description.* Endocarp ellipsoid, 7.2–9.9 mm long, 3.0–5.7 mm broad, 3.1–3.5 mm deep dorsiventrally, ornamented by ca. 10 longitudinal ribs, base rounded, apex pointed with stylar protrusion, unilocular, rounded-triangular in transverse section. Each germination valve has a pair of dorsal ifolds, resulting in a locule that may be T shaped in cross section.

*Comments.* This species is represented by only two specimens. The T-shaped or forked locule of these endocarps—as seen in cross section—appears to be a variant of the epsilon-shaped locule characteristic of the extinct genus *Langtonia*; these fruits are characterized by a pair of dorsal ifolds associated with each locule rather than by the single infold found in other mastixioids, as is best seen in the permineralized Eocene specimens (e.g., Manchester 1994). *Langtonia* has been found from the late Paleocene of Sand Draw, Wyoming (Tiffney and Haggard 1996), the Eocene Clarion Formation of Oregon (Manchester 1994), and the Eocene London Clay (Reid and Chandler 1933) floras. The Littleton endocarps are smaller than the bilocular *L. bisulcata* Reid & Chandler from Sand Draw (16.0–32.0 mm long; Tiffney and Haggard 1996).

**Genus**—Mastixicarpum Chandler emend. Manchester & Collinson

**Species**—Mastixicarpum hoodii Huegele & Manchester sp. n. (Figs. 4, 9F)

*Etymology.* Named after Glen Hood, who collected many of the specimens on which this investigation was based.

*Holotype.* DMNH EPL49425 (fig. 4A, 4B, 4D–4F).

*Type locality.* Littleton, Colorado, DMNH 8726, UF 19431.

*Other specimens examined.* DMNH EPL49300 (fig. 4C, 4I, 4J), 49301 (fig. 4H), 49362, 49365, 49391, 49422 (fig. 4G), 49423 (fig. 4K–4N), 49424, 49431, 49432, 49433, 49434, 49436, 49437, 49438, 49440. UF 19431-69562, 19431-62630 (fig. 9F), 19431-62635, 19431-81904, 19431-81905.

*Diagnosis.* Endocarp ellipsoidal, 8–13.5 mm long, 4.9–7.9 mm broad, 2.9–6 mm deep dorsiventrally, apically and basally rounded with a longitudinally running dorsal infold that intrudes a single boat-shaped locule with rounded base and apex, usually C shaped in cross section, sometimes inflected laterally. Germination valve ca. 4 mm wide, extending down the full length of the fruit or just short of the base. Surface ornamented by 15–18 distinct longitudinal ridges. Endocarp elliptical to almost circular in transverse section, wall 0.6–1.2 mm (average, 1.0 mm) thick.

*Comments.* These specimens resemble extant *Diplopanax* Handel-Mazzetti and the fossil genus *Mastixicarpum* in their unilocular endocarps with a well-defined germination valve marked by separation tissue, but they do not preserve the scattered ovular traces characteristic of both genera (Manchester and Collinson 2019). However, the type species of *Mastixicarpum* has fewer ovular traces than *Diplopanax*, and some specimens of *M. crassum* seem to lack these traces entirely (Manchester and Collinson 2019). Furthermore, extant *Diplopanax* fruits are nearly four times larger (ca. 45 mm long) than *M. crassum* (10–15 mm long). On the basis of favorable size comparisons with the type species of *Mastixicarpum* and the lack of paired ovular traces that characterize *Mastixia* Blume,

### Table 1

| Taxon                      | Occurrence                     | Apex                  | Locule no. | Valve length     | Maximum no. endocarp ridges per locule | Endocarp length (mm) |
|----------------------------|--------------------------------|-----------------------|------------|------------------|----------------------------------------|----------------------|
| A. littletonensis          | Early Paleocene of Colorado   | Rounded to acminate   | 4          | Short to elongate| 3                                      | 2.9–12               |
| A. obtrullata              | Paleocene of North America and China | Acuminate           | 3 (±4)     | Short            | Mostly smooth                          | ca. 7                 |
| E. jerseyensis             | Late Turonian of New Jersey    | Acuminate             | 3          | Short to elongate| 3                                      | 1.0–3.0              |
| E. vancouverensis          | Early Coniacian of Vancouver Island, British Columbia, Canada | Acuminate           | 3–4        | Elongate         | Ca. 6                                  |                      |
| E. hokkaidoensis           | Santonian of Hokkaido, Japan   | Rounded               | 4–5        | Elongate         | 1                                      | ...                  |

*a* The maximum number of ridges per locule refers to the greatest number of ridges found on the surface of the endocarp for each locule.
and allied genera, we assign the unilocular Littleton fossils to *Mastixicarpum*.

Fossil mastixioid fruits are found from the Maastrichtian through the Pliocene (Mai 1993; Hably and Erdei 2013) and were particularly diverse in the Early Eocene London Clay (Reid and Chandler 1933). The genus *Mastixicarpum* was initially described from the late Eocene of Hordle, England (Chandler 1926; Manchester and Collinson 2019). Although other European fossil occurrences were attributed to *Mastixicarpum*, it was later determined that most of these occurrences correspond to the extant genus *Diplopanax* (Eyde and Xiang 1990; Manchester and Collinson 2019). In North America, some fruits from the Eocene of Oregon (Manchester 1994; Manchester and McIntosh 2007) and the upper Eocene of Washington (Manchester et al. 2009) described as *Mastixicarpum* are likely *Diplopanax* instead. However, the well-preserved British Columbian Eocene fossil *Diplopanax eydei* Stockey, LePage & Pigg (1998) is distinct in its small size and inconspicuous vascular traces (similar to the type material of *Mastixicarpum*). The early Paleocene Littleton endocarps represent the oldest occurrence of this genus to date. These fruits are distinct from the Littleton *L. parva*, which has locules that are T shaped rather than C shaped in cross section.

**Fig. 3** *Langtonia parva* Huegele & Manchester sp. n. endocarps. A, B, DMNH EPL49439, ellipsoidal endocarp with rugulate sculpture. A, Isosurface rendering, lateral views. B, Successive transverse sections of endocarp from (from left to right) apex to base, showing single T-shaped locule, volume rendering. C–F, DMNH EPL49435. C, Successive transverse sections of a volume rendering from (from left to right) apex to base. D, Isosurface rendering, lateral views. E, Isosurface rendering, apical (top) and basal (bottom) views, showing ribbing and triangular outline. F, Successive longitudinal sections near edges (left, right) and through center (middle) of endocarp. Scale bar = 1.0 mm.

**Genus**—*Portnallia* Chandler  

**Species**—*Portnallia alexanderi* Huegele & Manchester sp. n. (Figs. 5, 9H)

*Etymology.* This species is named after Carl Alexander, who discovered and collected many plant and animal fossils from the Littleton locality.

*Holotype.* DMNH EPL49290 (fig. 5A, 5B).  
*Type locality.* Littleton, Colorado. DMNH 8726, UF 19431.  
*Other specimens examined.* DMNH EPL49274 (fig. 5C, 5E, 5F), 49291 (fig. 5D, 5G), UF 19431-62635 (fig. 9H).

*Diagnosis.* Endocarp ellipsoid to ovoid, 7.3–8.2 mm long, 4.2–4.5 mm broad, 3.9–4.9 mm deep dorsiventrally, ornamented by 12–21 gentle longitudinal ribs; base pointed to sometimes rounded, apex rounded or collar-like (slightly extended, truncated, and displaying three radially arranged depressions), trilocular, syncarpous, with three boat-shaped locules that are V shaped in transverse section. Each locule intruded by an elongate longitudinal infold visible on endocarp surface. Endocarp rounded-triangular in transverse section. Endocarp wall ca. 0.3 mm thick.
Fig. 4  *Mastixicarpum hooidii* Huegele & Manchester sp. n. endocarps. A, B, D–F, Holotype of *M. hooidii*, DMNH EPL.49425. A, Isosurface rendering showing ribbing and dorsal infold (far left), lateral views. B, Lengthwise tangential section from front, showing boat-shaped locule (light gray), volume rendering. C, I, J, DMNH EPL.49300. C, Isosurface rendering showing rugulate surface and longitudinal groove corresponding to the dorsal infold. D, Successive transverse sections through endocarp from apex (left) to base (right), showing visible separation tissue around germination valve (indicated by arrows) and single C-shaped locule. E, Longitudinal section through center of endocarp (far left), volume rendering, and isosurface rendering of boat-shaped locule in lateral (middle left), dorsal (middle right), apical (top right), and basal (bottom right) views. F, Isosurface rendering of apex (top) and base (bottom). G, DMNH EPL.49422 isosurface rendering showing dorsal infold. H, DMNH EPL.49301 isosurface rendering showing groove of the dorsal infold. I, Successive transverse sections from apex (left) to base (right) of the specimen in C, showing separation tissue (indicated by arrows) and locule. J, Isosurface rendering, apical view of the specimen in C. K–N, DMNH EPL.49423. K, Isosurface rendering, lateral views. L, Successive transverse sections near edges (left, right) and through center (middle). M, Isosurface rendering, apical (top) and basal (bottom) views. N, Successive transverse sections from apex (left) to base (right), showing locule and separation tissue (indicated by arrows). Scale bar = 1.0 mm.
Fig. 5  *Portnallia alexanderi* Huegele & Manchester sp. n. endocarps. A, B, Holotype of *P. alexanderi*, DMNH EPI.49290. A, Isosurface renderings: lateral (left four), apical (top right), and basal (bottom right) views. B, Successive transverse sections of volume rendering, showing three locules, each intruded by a dorsal infold; near apex (top), through middle (middle), and near base (bottom). C, E, F, DMNH EPI.49274. C, Isosurface renderings, lateral views (left four) and base (right). D, G, DMNH EPI.49291. D, Isosurface renderings of lateral views (left four), apex (top right), and base (bottom right). E, Successive transverse sections of volume rendering from apex (top) to base (bottom), showing the three curved locules. F, Longitudinal sections through center of endocarp (left), volume rendering; translucent isosurfaces of locules and endocarp in lateral view as in C (middle); isolated locules in apical view (top right); and locules and endocarp in apical view (bottom right). Locules highlighted in blue, green, and red in middle and top right view. Endocarp translucent in middle and bottom right view. G, Longitudinal (left) and transverse (right) section from original TIFF stacks. Scale bars = 1.0 mm; scale bar for A also applies to C, D, F, and G. Scale bar for E also applies to B.
Comments. These endocarps correspond to those of Portnallia, an extinct mastixiid genus with small multilocular endocarps, previously known only from the early Eocene London Clay flora (Chandler 1961). Like those of other mastixioids, the locules of Portnallia are boat shaped because of prominent longitudinal infolds corresponding to each carpel. Each locule bears a single seed that germinates via a valve that includes the infolded part of the endocarp. A peculiar feature of this species is the apical truncation with three terminal pits aligned with the locules (fig. 5A, 5D). This possibly marks a region where three styles may have protruded and where the perianth persisted, forming a collar around the epigynous fruit. In this feature, these fruits resemble some species of Symplocos, but there is no evidence of the central vascular channel or of the basal pit that characterizes that genus. Furthermore, the locules of Symplocos generally are not boat shaped, nor do they possess germination valves. As the original London Clay specimens of Portnallia lack preservation of the apex because of abrasion, we do not know whether the three apical pits are diagnostic for the genus or only for the new species erected here.

Portnallia is similar to the conspicuously ribbed, typically bi- to pentalocular fossil genus Eomastixia, but it differs in being much smaller than most Eomastixia species and lacking a thick, woody endocarp, resin canals, and visible separation tissue around its germination valve. Although the Littleton specimens have not demonstrated any obvious indication of resin cavities, this might be due to a lack of preservation, and many specimens of Eomastixia bilocularis—the type species for Eomastixia—have been found with resin canals “partially or completely missing” (Manchester and Collinson 2019, p. 61). Eomastixia bilocularis endocarps are also similar in size (ca. 11 mm long) to those of the Littleton Portnallia fruits. However, the thickness of the endocarp wall relative to the locule in E. bilocularis and other Eomastixia species is much greater than that of Portnallia species. Overall, the small size, thin endocarp wall, similarity in transverse section, and absence of resin canals and separation tissue suggest that these endocarps relate more closely to Portnallia than to Eomastixia.

Two species of Portnallia, P. bognoresensis Chandler (ca. 3.5–6 mm long) and P. sheppeyensis Chandler (6–7.5 mm long), have been described from the early Eocene of southern England; both are slightly smaller than the Littleton endocarps (Chandler 1961). The Littleton Portnallia is more elongate than these species but, overall, is more similar to P. bognoresensis in its ovoid shape and tendency toward three locules. Portnallia alexanderi marks the first recognition of this genus in North America.

Portnallia alexanderi differs from the Littleton M. hoodii in its trilocular endocarps, slightly smaller size, thinner endocarp wall, and lack of separation tissue outlining its germination valves. Furthermore, in transverse section, the locule limbs of P. alexanderi are straight or convex, while those of M. hoodii are slightly concave.

**Incertae Sedis A**

**Exemplary specimen.** DMNH EPI.49349 (fig. 6A–6C, 6F).

**Other specimens examined.** DMNH EPI.49350 (fig. 6D, 6E).

**Description.** Obpyriform, pentasymmetric fruit, 11.0–12.4 mm long, 9.5–7.7 mm in diameter, divided into five radial lobes. Y- or V-shaped cavities apparent in transverse section within each of the radial lobes. No obvious central vascular channel visible.

Comments. This fruit type might represent a pentalocular Eomastixia, but the preservation of tissues is too poor to confirm such an assignment by anatomy.

**Incertae Sedis B**

**Exemplary specimens.** DMNH EPI.49275 (fig. 7A–7D), 49277 (fig. 7F, 7J), 49396 (fig. 7K, 7L).

**Other specimens examined.** DMNH EPI.49276 (fig. 7I), 49292, 49293 (fig. 7O, 7P), 49294, 49295 (fig. 7S, 7T), 49332, 49333, 49334, 49335, 49336, 49337 (fig. 7E, 7G, 7H), 49338, 49342, 49353, 49354, 49355, 49357, 49358, 49359, 49363, 49367, 49389, 49390 (fig. 7Q, 7R), 49394, 49415, 49418, 49420 (fig. 7M, 7N), UF 19431-81893, 19431-81895, 19431-81896, 19431-81897, 19431-81898, 19431-81899, 19431-81900, 19431-81902, 19431-81903, 19431-81906, 19431-69559, 19431-69560, 19431-69561, 19431-62633, 19431-62632, 19431-62634, 19431-62636, 19431-62637 (fig. 9G).

**Description.** Globose to ellipsoid disseminule, sometimes disk shaped (because of compression), 6.5–16.0 mm long, 6.1–13.0 mm broad, 4–10 mm deep, sometimes ridged, bearing a pedicel-like stalk that is nearly circular in cross section. Small circular aperture sometimes present. A short longitudinal suture sometimes occurs along rim of the disseminule. Putative seed coat ca. 0.6 mm thick, surrounding the disseminule, surrounded by possible pericarp tissue.

Comments. Three different morphotypes of this kind of disseminule have been found, possibly representing three different preservational states of deterioration. In the first type (type I; fig. 7A–7E, 7G, 7H), three layers of what may putatively be the seed, seed coat, and pericarp are preserved. Sometimes the seed coat is slightly deteriorated, caving inward at certain points, but it is mostly continuous and has a fibrous texture. In the second type (type II; fig. 7F, 7L, 7J), the deterioration is so great as to have disarticulated most parts of the testa into fragments. The surfaces of these first two types are smooth. The third type (type III; fig. 7K–7T), by contrast, has ca. 15–18 broad ridges and three to five distinct layers within it (see fig. 7L, 7P). Some of these layers appear as though they may correspond to the three layers of the first two morphotypes. These relatively large, round disseminules are slightly reminiscent of Arecaceae. However, we were unable to document diagnostic features of palm fruits such as embryo position or germination caps (see Matsunaga et al. 2019 for examples illustrated with µCT).

**Incertae Sedis C**

**Exemplary specimen.** DMNH EPI.49289 (fig. 8A–8D).

**Description.** Disseminule pyriform, almost bilaterally symmetric, 5.1 mm long, 3.8 mm wide, 3.1 mm deep, with narrow longitudinal ridge or wing in plane of bisymmetry; slightly and highly sculpted surface ornamentation of horizontal ridges intersecting with the longitudinal ribs. Upper aperture circular, ca. 0.4 mm wide, recessed; lower aperture not well defined, ca. 1 mm wide, recessed. Wall ca. 0.5 mm thick, encasing two inner chambers that may or may not be connected at the center.
The symmetry and highly sculptured surface ornamentation of this morphotype are reminiscent of Juglandaceae. However, a longitudinal suture separating the nutshell into two halves, which would be expected of that family, is not apparent in this specimen. Although there are apertures at both ends of the disseminule, there is no central vascular channel connecting them.

**Incertae Sedis D**

**Exemplary specimen.** DMNH EPL49349 (fig. 8E).

**Other specimens examined.** DMNH EPL49312, 49313, 49314 (fig. 8H), 49316, 49361, 49366, 49376.

**Description.** Disseminule ellipsoid, truncated basally, pointed apically, 3.0–4.7 mm long, 2.0–4.0 mm wide, 1.3–2.2 mm thick, bearing faint longitudinal ridges. Surface smooth. Apex bears a faint triangular depression. Wedge shaped in side view.

**Comments.** No internal structure has been preserved in these specimens.

**Incertae Sedis E**

**Exemplary specimen.** DMNH EPL49411 (fig. 8F, 8G).

**Description.** Disseminule ellipsoid, 5 mm long, 3.3 mm wide, 2 mm thick, pointed at apex, rounded at base, with crinkled, rough surface ornamentation. Base bears a small elliptical aperture. Apex possibly exhibits a styal scar.

**Incertae Sedis F**

**Exemplary specimen.** DMNH EPL49304 (fig. 8I).

**Other specimens examined.** DMNH EPL49303.

**Description.** Disseminule thin, disk shaped, 2.7–3 mm long, 2.3–2.4 mm wide, 1.0–1.2 mm deep, with two pointed protrusions on its lateral edges.

**Comments.** These small disseminules contain a single chamber (fig. 8I).

**Incertae Sedis G**

**Exemplary specimen.** DMNH EPL49387 (fig. 8J).

**Description.** Disseminule thin, roughly obpyriform and asymmetric in face view, convex concave (S-shaped) in lateral view, 3.7 mm long, 2.4 mm wide, 1 mm thick.

**Comments.** No internal morphology is preserved for this specimen.

**Incertae Sedis H**

**Exemplary specimen.** DMNH EPL49400 (fig. 8K).
Fig. 7  Incertae Sedis B, large round disseminules. A–E, G, H, Type I: large round disseminules with continuous outer layer. A–D, DMNH EPL49275 isosurface rendering; colors indicate different layers. A, Broken face of disseminule, showing three layers. B, Unbroken side of disseminule: middle fibrous layer (left) and inner homogeneous layer (right). Circular pore indicated by arrow near putative apex. C, Putative apex of each layer. Outer green layer (left) shows a small elliptical depression. D, Lateral views of each layer. E, G, H, DMNH EPL49337, with broken outer layer. E, H, Isosurface renderings. G, Cross sections through middle (top) and edge (bottom) of disseminule, volume rendering. F, I, J, Type II: large round disseminules with deteriorated inner layer. F, J, DMNH EPL49277. F, Oblique section from original TIFF images produced by a micro-computed tomography scan. I, DMNH EPL49276 isosurface rendering, lateral views, showing faint depression at putative apex. J, Isosurface rendering, lateral views. K–T, Type III: large round disseminules with longitudinal ridges. K, L, DMNH EPL49396. K, Lateral views (left) and apical view (right), showing pedicel-like structure. I, Successive transverse sections from putative apex (left) to base (right) of disseminule. M, N, DMNH EPL49420 isosurface rendering. M, Putative apex (left) and base (right). N, Side views. O, P, DMNH EPL49293. O, Isosurface rendering, showing longitudinal ridges and circular pore (arrow) near apex, lateral views. P, Longitudinal sections perpendicular to each other. Q, R, DMNH EPL49390. Q, Successive longitudinal sections near edges (left, right) and center (middle). R, Isosurface rendering, showing thin layer with ridges. S, T, DMNH EPL49295 isosurface rendering. S, Side view. T, Top (left) and bottom (right) views. Scale bar = 1.0 mm.
Fig. 8  Incertae Sedis C–I. A–D, Incertae Sedis C, DMNH EPL.49289, disseminule with rugose ornamentation. A, Isosurface rendering, lateral views. B, Successive longitudinal sections through middle (left) and edge (right), showing inner chambers. C, Isosurface rendering of putative apex (left) and base (right), showing small circular pore at apex and gap at base. D, Successive transverse sections from apex (left) to base (right). E, H, Incertae Sedis D, small pointed disseminule, isosurface renderings. E, DMNH EPL.49419, showing small apical depression, lateral (left two), apical (top right), and basal (bottom right) views. F, G, Incertae Sedis E, DMNH EPL.49411, small ornamented disseminule. Isosurface renderings showing many small ridges and apical and basal dimples. F, Lateral views. G, Apical (top) and basal (bottom) views. H, DMNH EPL.49314. I, Incertae Sedis F, DMNH EPL.49304, possibly rhamnaceous disseminule. Isosurface rendering, lateral (left three) and side (upper right) views. Transverse section, volume rendering (bottom right). J, Incertae Sedis G, DMNH EPL.49387, small disseminule with inflection. Isosurface rendering, lateral views. K, Incertae Sedis H, DMNH EPL.49400, small winged disseminule, isosurface rendering, lateral views. L, Incertae Sedis I, DMNH EPL.49379, strongly ridged disseminule. Isosurface rendering, lateral (left four), apical (upper right), and basal (bottom right) views, showing prominent ridges and apical and basal pores. Scale bar = 1.0 mm.
Fig. 9  Incertae Sedis J, *Mastixicarpum hoodii*, Incertae Sedis B, and *Portnallia alexanderi* photographs of surface views and physical sections under reflected light. A–E, Incertae Sedis J, UF 19431-81901. A, B, Front and back views. C, D, Side views. E, Section through center of disseminule. F, *Mastixicarpum hoodii*, UF 19431-62630, transverse section showing single locule (gray) and dorsal infold. G, Incertae Sedis B, UF 19431-62637, section through center of disseminule. H, *Portnallia alexanderi*, UF 19431-62635. Tranverse section of broken specimen shows two remaining C-shaped locules (brown, white) and longitudinal infolds. Scale bars for A and E = 5.0 mm; scale bar for A also applies to B–D. Scale bars for F–H = 1 mm.
Description. Obovate in outline, 1.6 mm thick, with curved edges, rounded at base, with two longitudinally running lateral wings. Comments. No internal morphology preserved.

**Incertae Sedis I**

Exemplary specimen. DMNH EPL 49379 (fig. 8A). Description. Disseminule flattened, with 3.4 mm wide, 1.9 mm thick, with ca. six continuous arching longitudinal ridges that extend from the apex to the base. Comments. No internal morphology preserved.

**Incertae Sedis J**

Exemplary specimen. UF 19341-81901 (fig. 9). Description. Disseminule large (ca. 30 mm long, 27 mm wide, 13 mm thick), ellipsoid, thick walled. Comments. This specimen resembles Incertae Sedis B in external shape. However, it is substantially larger than any other disseminule in the Littleton flora. A physical transverse section of the specimen shows what appears to be a single internal chamber and a thick wall (ca. 2–3 mm).

**Discussion**

Incertae Sedis B is the most abundant member of the Littleton flora, representing ca. 30% of the flora, followed by *Amersinia* (ca. 27%), *Mastixicarpum* (ca. 13%), *Kingsboroughia* (ca. 11%), and the remaining taxa (each of which individually makes up <5% of the flora; table 2). The abundance of cornalean fruits (including *Amersinia* and *Mastixicarpum* as well as *Langtonia* and *Portnallia*), together representing more than 40% of the flora, and of Sabiaceae (*Kingsboroughia*) is striking, possibly an indication that fruits with indurated endocarps were favored in preservation.

**Comparison with Other Paleocene Floras**

We compared the Littleton flora with three other floras known from the Paleocene of North America: the Sand Draw flora of Wyoming, the Almont flora of North Dakota, and the Newell's Nook flora of Montana. Among these, the Almont flora, with about 28 fruit and seed types, has been the most thoroughly documented. The late Paleocene (likely Tiffanian; Hartman and Kihm 1991) Almont flora of the Sentinel Butte Formation in North Dakota (Crane et al. 1990; Manchester et al. 1999) is known from leaves and pollen as well as from fruits and seeds (as summarized by Zetter et al. 2011). Although the Almont flora shares *Kingsboroughia rostellata* in common with the Littleton flora, we did not encounter other shared fruit and seed species. A unilocular mastixioid fruit similar to *Mastixicarpum* is common in the Almont assemblage (K. Pigg and S. Manchester, personal observation), but it is larger than the Littleton mastixioid taxa.

An unpublished fruit and seed flora associated with the Tiffanian or Torrejonian vertebrate fauna of the Fort Union Formation at Newell's Nook, Montana (Robinson and Honey 1987), also shares *K. rostellata* in common with the Littleton flora. However, the Newell's Nook flora has several other elements in common with the Almont flora, such as Cercidiphyllaceae, Hamamelidaceae, Juglandaceae, possibly Mastixiaceae, Platanaceae, and others (S. Manchester and I. B. Huegel, unpublished manuscript).

Another late Paleocene carpopollina from the Fort Union Formation is located in Sand Draw, Wyoming. This flora includes *Melisosia*, *Platanus* L., and other angiosperms, along with members of Mastixiaceae (*Mastixia* and *Langtonia*) and the nyssoid *Davidia* (Tiffney and Haggard 1996; Tiffney and Manchester 2019). Although there are a few shared taxa between the early Paleocene Littleton flora and these late Paleocene carpophorals, their taxonomic composition is more different than similar, indicating a change in floristic composition and environment over several million years. However, there are too few Paleocene fruit and seed floras to draw firm conclusions at this stage. Several families, including Betulaceae, Hamamelidaceae, Juglandaceae, Menispermaceae, Platanaceae, and Taxaceae, in addition to nyssoids, occur in these three late Paleocene localities, but only Sabiaceae (*Kingsboroughia* and/or *Melisoma*) are known from all four localities.

Within the Denver Basin, nearly 150 fossil leaf localities, ranging from the Late Cretaceous through the early Eocene, have been investigated. Most of these, like the Littleton site, are from Paleocene and Cretaceous units of the Denver Formation, or the “D1 sequence” (Johnson et al. 2003). The lower Paleocene localities (P-D1) of the Denver Formation primarily occur in three regions: east, central, and west (Johnson et al. 2003). P-D1 East (Denver Lignite Zone) represents mostly fluvial and lacustrine angiosperm floras dominated by *Populus* *nebrascensis* Newberry; “Cornophyllum” *neberryi* (Hollick) McIver & Bainger (syn. *Metapanophyllum nebrascense* Schimp) Manchester;
Dicotylodyum anomulum (Ward) Hickey; Paranyphaea crassifolia (Newberry) Berry; Zizyphoides flabella (Newberry) Crane, Manchester & Dilcher; palm and Platanites Forbes swamp floras; and Taxodiaceae swamp floras (Barclay et al. 2003; Johnson et al. 2003; Manchester 2014). P-D1-Central sites are mostly fluvial deposits and commonly include ferns and palms alongside other angiosperms such as “Artocarpus” lessigiana (Lesquereux) Knowlton, “Ficus” planicostata Lesquereux, “Rhambas” golddana Lesquereux, and “Ziziphus” fibrillosus (Lesquereux) Lesquereux (Johnson et al. 2003). P-D1-West is the richest and best studied of the three areas, with roughly 68 and 98 different morphotypes having been observed from the Scotty’s Palm fossil plant site and the Castle Rock site, respectively (Johnson and Ellis 2002; Reynolds et al. 2002; Ellis et al. 2003; Johnson et al. 2003). The physiognomy and taxonomic content of this flora have been interpreted as representative of a rain forest with moderately high diversity that included members of Platanaceae, Lauraceae, Elaeocarpaceae, Tiliaceae, Sterculiaceae, and Urticaceae. Compared with Littleton, the Scotty’s Palm and Castle Rock localities have drastically greater species richness. Although Mastixiaceae and Sabiaceae have not been confirmed in other Paleocene floras of the Denver Basin, the environment preferred by modern Mastixiaceae and Sabiaceae relatives (van Beusekom 1971; Eyde and Xiang 1990) includes warm, wet, swampy conditions similar to those hypothesized for other floras in the Denver Basin. Prominent components of other early Paleocene floras in the Denver Basin, such as Platanaceae, Juglandaceae, and Betulaceae, were possibly represented in the Littleton flora but have not been preserved or discovered; the conditions that would lead to three-dimensionally preserved fruits and seeds are often very different from those that would preserve thin leaf or achene material. The differences in floras could also represent regional variation within the Denver Basin. Even among vertebrate localities of similar age in the Denver Basin, taxonomic composition can vary widely (Eberle 2003). It should also be noted that modern forests, even in tropical environments, can often be locally dominated by one or a few species (Nascimento et al. 1997; Steege et al. 2013; Kazmierczak et al. 2016). An example of this can be found in the Denver Basin at the Sick of Sycamores site in P-D1-West, which yielded only 20 morphotypes out of 1092 specimens, with 1035 of these leaves belonging to a single species, Platanites marginata (Lesq.) Johnson (Johnson et al. 2003). Such local dominance of a few taxa may have also been the case for the Littleton flora.

**Disseminule Size**

With the exclusion of Incertae Sedis J, measurement of 131 specimens from the Littleton flora yielded an average volume of 224.0 mm³ and a median volume of 149.2 mm³, with volume ranging from 7.2 mm³ for the smallest disseminules (i.e., Incertae Sedis F) to 1784.6 mm³ for the largest (i.e., the possibly arecaceae Incertae Sedis B; table 2). These numbers are similar to but larger than the average (129 mm³) and range (1.2–731 mm³) of disseminule size reported by Tiffney (1984) for the late Paleocene Woolrich and Reading Beds of England treated by Chandler (1961). However, the inclusion of Incertae Sedis J would increase the range of Littleton volumes to 7.2–5513 mm³. Despite having larger disseminules than the Wool-rich and Reading Beds, the Littleton flora overall seems to fit into the general trend of fruit and seed size increasing over time (Tiffney 1984) until the late Eocene (Eriksson et al. 2000). Other late Paleocene and early Eocene floras treated by Eriksson et al. (2000), in contrast to the Woolrich and Reading Beds, have much larger median fruit sizes (ca. 100–800 mm³) and a greater size range (ca. 7–500,000 mm³) than the Littleton flora. However, the only early Paleocene flora (63 Ma) considered by Eriksson et al. (2000), Gonna-Walkmühlz II, has a median fruit size of ca. 10 mm³, a median seed size of 5 mm³, and ranges of fruit sizes (ca. 0.9–400 mm³) and seed sizes (ca. 0.9–5 mm³) that are smaller than those of the Littleton flora. Tiffney (1984) observed that Cretaceous floras had substantially smaller seed size ranges and averages than Tertiary floras. However, Eriksson et al. (2000), using an increased sample size, suggested that the median fruit and seed size ranges gradually increased from the late Cretaceous to the Paleocene, with the late Paleocene and early Eocene representing the highest peak in these sizes prior to a gradual decrease in the late Eocene. Although the median, average, and range of fruit and seed sizes within the Littleton flora are larger than those in some early Paleocene and late Paleocene sites (e.g., Gonna-Walkmühlz II, Woolrich and Reading Beds; Tiffney 1984; Eriksson et al. 2000), the Littleton disseminules are larger than those of Cretaceous floras and smaller than those of most late Paleocene and early Eocene floras. The Littleton flora therefore fits into the general trend of increasing fruit and seed size from the Cretaceous through the late Eocene but suggests that this increase may have been more rapid than previously supposed.

As has been observed in modern floras, seed size in fossil floras of the Early Cretaceous through the Pliocene has been found to be largest at equatorial latitudes and to decrease toward the poles (Sims 2010). Reconstruction of past continental positions (estimated from http://portal.gplates.org/map; http://www.odsn.de/odsn/services/paleomap/paleomap.html) suggests that the Littleton flora was at roughly 46°–43°N paleolatitude, which is a similar, albeit slightly higher, latitude than where it is today (39°N). Sims (2010) found no significant correlation between seed size and latitude during the Cretaceous, although significant correlations could be found for Tertiary localities. Sims (2010) interpreted this change as an effect of the end-Cretaceous mass extinction event that drastically changed plant communities. As the Littleton flora is from the earliest Paleocene, it is unclear whether it was influenced by latitude in the manner that other Tertiary floras were or whether it was more like the preceding Cretaceous floras. The Woolrich and Reading Beds were at a latitude of ca. 46°N, while the Gonna-Walkmühlz II was at a latitude of 47°N (Sims 2010). As these latitudes are similar to the position of the Littleton flora, the difference in fruit and seed size among these floras is probably not due to latitudinal variation.

**Frugivory and Dispersal Modes**

Disseminule size has been shown to correlate roughly with dispersal modes. Larger disseminules tend to be biotically dispersed, while smaller disseminules may be either biotically or abiotically dispersed (Tiffney 2004). Animal dispersers could have eaten the flesh of the Littleton fruits while discarding.
their hard seeds or endocarps, or they might have ingested the whole fruits and later defecated their seeds (see Levey 1987; Herrera 1989). For many of the small disseminules in the Littleton flora (i.e., Incertae Sedis D–G, 1), either of these situations or abiotic transportation may have been possible. Only for Incertae Sedis H, which possesses small wings, would it appear that wind dispersal is most likely. Unfortunately, fleshy tissue is not readily preserved in most carpo floras, including in the Littleton flora, so inference of dispersal modes may be better interpreted through comparison with modern relatives (Tiffney 2004). Living relatives of Mastixiacaeae are known to be dispersed by rodents and birds (Eyde and Xiang 1990), and both modern and fossil mastixioid endocarps have been found bored or gnawed by rodents (Eyde and Xiang 1990; Huegule and Manchester 2019). However, none of the Littleton mastixioids bear any evidence of predation. These mastixioids were possibly dispersed by birds of the smaller type (Levey 1987), which separate or mash the soft outer fruit layers of these fruits before dropping the hard whole endocarps. Another possibility is that these fruits were eaten whole and the hard endocarps remained intact after passing through the digestive tracts of mammals or birds of the gulper type (Levey 1987; Herrera 1989); this might be a likely possibility, considering the small size of the Littleton Mastixia ceae. Finally, such damaged fruits might have been masticated or digested so completely as to be unrecognizable or not readily preserved. Similar possibilities could be used to explain the lack of frugivorous damage on other Littleton disseminules. Amer sina, similar to Mastixiaceae and Nyssaceae, may have been dispersed by birds and small mammals. Extant Melosoma, closely related to the Littleton Kingsboroughi, has been also found to be scattered and hoarded by small rodents (Wenny 2000).

Although frugivorous birds may have been present as early as the Late Cretaceous, major radiations of frugivorous birds may not have occurred until the Eocene with the origination of lineages such as the Psittaciformes (parrots), Cuculiformes (including turaco), Coraciiformes (including hornbills), and Passeriformes (perching birds; Eriksson 2016). However, many of these Eocene records are sparse or controversial, and early members of these avian lineages may have had general diets rather than frugivorous ones (Eriksson 2016). As such, it is uncertain whether frugivory was a common avian feeding strategy during the Paleocene. The Littleton fauna that co-occurs with the flora has no records of birds, so it is unclear what role they may have played in interacting with the flora. Similarly, rodents and primates did not become important fruit dispersers until the early Eocene (or possibly the late Paleocene; Eriksson 2016) and are likewise not recorded among the Littleton fauna.

The vertebrate fauna at the Littleton site may therefore be informative about what particular vertebrates might have consumed and/or dispersed the flora. Although there is no evidence of bite marks on the fruits themselves, unlike in some late Eocene localities (Collinson and Hooker 2000; Huegule and Manchester 2019), the specialized occlusal features on the teeth of co-occurring mammals can be used to infer diets. Body size, “roughly shrew- to indri-sized” and no greater than 8 kg for the Littleton mammals (Dewar 2003, p. 3), can also be useful as a loose proxy for metabolism. In a study on teeth wear, teeth shape, and inferred body size, Dewar (2003) suggested that most mammalian species of this fauna were likely omnivorous and had preferences for “soft-tough” and “hard-brittle” food types. The soft-tough type includes foods masticated through a cutting, shearing, and piercing motion; these foods include soft animal tissues, some insects, and possibly young foliage (Dewar 2003). The hard-brittle type, on the other hand, includes foods reduced through a crushing, splitting, or grinding motion; these foods include bone, some insects, seeds, nuts, roots, some tubers, and unripe fruits. The smaller mammalian species with slender sectorial teeth, Baiocodon sp., Conacodon harbourae Eberle & Lillegraven, Oxycleaenus sp., and Peradectes pusillus Matthew & Granger, were thought to consume the soft-tough food type (Dewar 2003). Other species, Alticormus gazini Eberle & Lillegraven and Baiocodon denverensis Gazin, two larger members of the fauna, were interpreted as consuming the hard-brittle food type (Dewar 2003). The preference for these food types may possibly be representative of a mammal population with stronger tendencies for frugivory than for grazing or other kinds of herbivory. Most foliage would likely fall under the tough-fibrous food type, which would require dominant cutting and shearing motions. Although Baiocodon sp. had a slightly greater shearing phase than grinding phase and may have consumed thin plant material, most Littleton mammals likely consumed insects (especially the case for the smallest species in this fauna, P. pusillus) and other nonfoliar plant matter of the soft-tough and hard-brittle food types, possibly including fruits. However, the tendency toward soft-tough and hard-brittle food types suggests that the Littleton mammals, if frugivorous, may have preferred hard and brittle or fibrous and woody fruits over soft, pulp-rich ones, the latter of which would fall into the turgid food type. Dewar (2003) has suggested that the most abundant species within the Littleton fauna, B. denverensis, likely consumed large quantities of tough foods and foods with abrasive materials.

Although there is no direct evidence of predation on the Littleton fruits and seeds to suggest that they were consumed or dispersed by these co-occurring mammals, the fruits of larger Littleton species, such as Mastixicarpum, may have been fibrous and woody with a surrounding leathery mesocarp, similar to the fruits of living Diplopanax (Eyde and Xiang 1990). Other Cornales in this flora, like living Mastixia and Nyssa, may have been somewhat fleshy, but we lack evidence to know whether they had enough soft pulp tissue to fall under the turgid food type. These morphologies would support the diet of soft-tough food types suggested by Dewar (2003) for many of the Littleton mammals. The smaller Littleton disseminules (e.g., Incertae Sedis D–G, 1) may have possibly been derived from large, pulp-rich, many-seeded fruits (see studies on frugivorous members of order Carnivora; Herrera 1989), but the inferred diets of co-occurring mammals do not directly support the presence of fleshy, soft fruits of the turgid food type. Some studies have shown that small seeds are more likely to survive the digestive tract of mammal groups (e.g., suids and cercopithecid monkeys) than large seeds are (Herrera 1989 citing Gautier-Hion 1984 and Génard and Lescourret 1985). However, Herrera (1989) found that high percentages (over 90% for most species) of seeds consumed by carnivores, regardless of seed size, could survive their digestive systems. As such, it is uncertain whether smaller seeds were advantageous in surviving the digestive systems of Littleton fauna.

The advent of fleshy fruits occurred in the Late Cretaceous (ca. 80 Mya) as fruit types diversified and fruit and seed size
increased (Eriksson 2016). Like fruit and seed size, the diversity of fruit forms peaked—and fleshy forms became abundant—in the early Eocene (ca. 55–50 Mya; Collinson and Hooker 2000; Eriksson 2016). Plesiadaptiforms (early primate relatives) may have influenced this period of fruit evolution from the Late Cretaceous to the Paleocene (followed later by euriprimates in the early Eocene), but multibaccate species have been considered the most important agents of fruit dispersal during this phase of fruit and seed evolution (Eriksson 2016). However, of the 21 mammalian species found at the Littleton site, only 6 are multibaccate, while the other 15 species are holotherians (i.e., marsupial and placental mammals; Middleton and Dewar 2004). Holotherians are the most abundant members of the fauna (e.g., *B. denverensis*) and include those studied by Dewar (2003) that had soft-tough and hard-brittle diets (including the single marsupial *P. puillus* and the placental mammals *A. gazini*, *Baiconodon* sp., *B. denverensis*, *C. harbourae*, and *Oxycaecus* sp.). If they were frugivorous, this suggests that holotherians may have had a greater influence on fruit dispersal and evolution in the Paleocene than was previously thought.

Conclusions

Although carpofloras are rare in the North American fossil record, they are valuable for their utility in taxonomic identification and in reflecting plant-animal interactions. The Littleton flora represents the first three-dimensionally preserved fruit and seed assemblage from the early Paleocene of North America and is additionally valuable for its co-occurrence with a well-documented and diverse Puercon vertebrate fauna, as well as for its proximity to other megafaunal floras of similar age in the Denver Basin. Our study of 213 fruits and seeds from this site has shown a surprising abundance of species representing the Cornales and Sabiaceae and introduces the earliest-recorded occurrences of certain genera (e.g., *Mastixicarpum* and *Portnallia*) and extended geographic ranges for others (e.g., *Amersinia*, *Portalalia*). Although the Littleton flora does not share many taxonomic similarities with other Paleocene carpofloras, *Kingsboroughia* is a recurring element in these assemblages. Taxonomic overlap with other Paleocene floras in the Denver Basin is minimal, but modern-day relatives of the Littleton taxa occupy environments similar to those inferred for previously described Paleocene Denver Basin leaf and wood assemblages. The fruit and seed sizes observed here conform with previously documented trends of increasing size from the Late Cretaceous to the Eocene, but the Littleton flora seems to have slightly larger disseminule sizes than the contemporary early Paleocene Gonna-Walkmühlz II flora and the late Paleocene Woolrich and Reading Beds flora (Tiffney 1984; Eriksson et al. 2000). Previous studies on dentition have suggested that the Littleton mammals preferred hard-brittle and soft-tough food types (Dewar 2003). We infer that the drupaceous fruits of Mastixicaceae and Sabiaceae are consistent with these suggested food types and that the Littleton fauna might have included animals adapted for frugivory, particularly of woody fruits in preference to foliage. We also record here several other fruit morphotypes that hopefully will be identified in future studies. Further collection from this site may improve our understanding of this flora, life in the early Paleocene, and the evolution of modern fruit and seed morphology.

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