THE EARLY MIDDLE EOCENE WAGON BED CARPOFLORA OF CENTRAL WYOMING, U.S.A.

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Abstract: The early middle Eocene Wagon Bed fruit and seed flora of central Wyoming encompasses nine morphotypes that are assignable to extant genera (*Alangium*, *Aphanathe*, *Canarium*, *Carya*, *Celtis*, *Iodes*, *Mastixia*, *Nyssa*, *Pleiogynium*), four that are assignable to extinct genera in extant families (*Chandlera*, Menispermaceae; *Coryloides*, Betulaceae; *Pentoperculum*, Anacardiaceae; *Saxifragispermum*, Salicaceae) and one morphotype potentially assignable to an extant family (Pandanaceae). At least 11 morphotypes remain unidentified due to incomplete characters, although some exhibit features suggestive, but not definitive, of extant families (e.g., Euphorbiaceae, Lauraceae, Nymphaeaceae, Rosaceae). Individual taxa exhibit paleobiogeographic links with the Eocene floras of the west coast of North America, as well as with those of the Eocene of Europe. Together with previously described pollen and woods, these fruits and seeds indicate a mixed evergreen and deciduous forest, existing under moist circumstances, possessing primary taxonomic affinities with extant paratropical taxa of the Old World.

Introduction

The depositional basins of Wyoming have long provided a range of information on the evolution of the North American Paleogene flora (Brown 1962, Leopold and MacGinitie 1972, MacGinitie 1974, Wing et al. 1995, Gemmill and Johnson 1997, Davies-Vollum and Wing 1998, Wilf 2000, Manchester and Hermsen 2001, Manchester 2014, Allen et al. 2015). These floras contribute to our concept of a widespread paratropical forest at midlatitudes of the Northern Hemisphere in the early Tertiary (Wolfe 1977, 1978).

The Wagon Bed Formation of the Wind River Basin of Wyoming has yielded fossil vertebrates (Van Houten 1964, Love 1970, Emry 1975, Krishtalka et al. 1987), but previously reported plant material has been limited. A single specimen of "*Carpolithes*" BRONGN. was identified by R. Brown (in Van Houten 1964) with the observation that it was "a common fossil in the Green River Formation." Leaf fossils from a carbonaceous shale were identified by H. MacGinitie (in Love 1970) as including *Zelkova* SPACH, "*Quercus*" L. and *Liquidambar* L. Associated pollen (identified by E. B. Leopold in Love 1970) included *Carya* NUTT., *Quercus*, *Zelkova-Ulmus* L., *Platycarya* SIEBOLD et ZUCC., *Juglans* L., *Nymphaea* L. and *Rhus* L. Brown (1959) mentioned some

biwinged fruits and problematic stem impressions from siltstone of the same formation. The winged fruit specimen was later identified as *Illigera eocenica* MANCHESTER et E.O'LEARY (Hernandiaceae; Manchester and O'Leary 2010).

In 1966, R. A. Scott of the United States Geological Survey was introduced to a new assemblage of silicified fruits and seeds at Oil Mountain located in the NE 1/4 of section 25, T 33N, R 95W, (Lat. 42° 48′ 34.99″ N, Long. 108° 09′ 01.07″ W; USGS Paleobotanical Locality D3795) by a local resident, Mrs. Novotny. While the source rock was initially identified as the Aycross Fm., it was subsequently confirmed as the Wagon Bed Fm. by N. Denison (Pers. comm. to R. Scott, 4/16/69). Scott also sampled the sediment for palynological investigation. The resulting spore and pollen flora was investigated by E. B. Leopold (Leopold and MacGinitie 1972; Tab. 1) and included 21 taxa that reflected an "evergreen, broad-leaved, sclerophyllous forest" that was similar to the known early middle Eocene floras of Wyoming (MacGinitie 1974). Subsequently, J. H. Jones collected and described several fossil woods from this and adjacent localities (Fierro and Jones 1990, Issa and Jones 1990, Salami and Jones 1990). However, the fruit and seed material remained undescribed. The locality was revisited by Manchester and Tiffney in 1995 and Jones and Manchester

Table 1. Presence of genera identified from the Wagon Bed flora from fruits and seeds (this paper), pollen (Leopold and MacGinitie 1972) and wood ([1] Salami and Jones 1990, [2] Issa and Jones 1990, [3] Fiero and Jones 1990, [4] Jay H. Jones, pers. comm.). Pollen taxa denoted by [#] were described by Leopold (in Love 1970) but not subsequently reported by Leopold and MacGinitie (1972). *Illigera* BLUME was reported from another locality in the Wagon Bed Formation by Manchester and O'Leary (2010).

Family	Fruit/seed representative	Pollen representative	Wood representative
?Nymphaeaceae	Possible seeds	Nymphaeaceae[#]	–
Hernandiaceae	*Illigera**	–	–
?Lauraceae	"*Laurocarpum*"-like	–	–
?Pandanaceae	Genus indet	–	–
Arecaceae	–	Palmae indet.	–
Menispermaceae	*Chandlera*	Menispermaceae?	–
Gunneraceae	–	*Gunnera*	–
?Euphorbiaceae	Possible seed	–	–
Salicaceae	*Saxifragispermum*	–	–
Cannabaceae	*Aphananthe*, *Celtis*	–	*Trema*-like[1]
Moraceae	–	*Morus* type	–
Rhamnaceae	–	–	Rhamnaceae indet.[4]
Rosaceae	?Rosaceae – cf. *Prunus*	–	*Prunus* indet.[4]
Ulmaceae	–	*Ulmus/Zelkova*	–
Betulaceae	*Coryloides*	*Alnus*?	
Fagaceae	–	*Quercus*[#]	*Quercus*[2]
Juglandaceae	*Carya*	Juglandaceae (Extinct), *Carya*, *Engelhardtia/Alfaroa/Oreomunnea*, *Platycarya*[#], *Juglans*[#]	–
Anacardiaceae	*Pentoperculum*, *Pleiogynium*	*Rhus*	–
Burseraceae	*Canarium*	*Canarium* type	cf. Lythraceae/ Sapindaceae/ Melastomataceae/ Burseraceae[3]
Rutaceae	–	–	cf. Rutaceae/ Campanulaceae[4]
Aceraceae	–	–	*Acer*[4]
Sapindaceae	–	*Cardiospermum*	–
Malvaceae s.l.	–	"Bombacaceae indet.", "*Sterculiaceae* indet.", *Triumfetta-Grewia*	–
Cornaceae	*Alangium*, *Mastixia*, *Nyssa*	–	cf. Nyssaceae/ Styracaceae[4]
Eucommiaceae	–	*Eucommia*	–
Apocynaceae	–	*Trachelospermum* type	–
Icacinaceae	*Iodes*	*Phytocrene, Iodes* type	–

in 2008 without success to locate additional fruits and seeds, although a few chalcedony twig casts, preserved in a manner similar to the earlier-collected fruits, were observed. Given that the fragments of wood were collected on the surface of the sediment, we assume the same was true of the fossil fruits and seeds. Because the locality is surrounded by Wagon Bed Formation, including topographically higher adjacent strata from which these resistant chalcedony specimens might have eroded, we believe that, even if not "in situ", the fossils Scott collected derive from the Wagon Bed Formation.

Stratigraphy

The flora occurs in the Wagon Bed Formation on the southern margin of the Wind River Basin (Keefer 1970). The Wagon Bed Formation was initially defined by Van Houten

(1964) for a series of beds that had previously (e.g., Keefer 1965) been treated as "transitional" between the early Eocene Wind River and Oligocene White River Formations. The sediments included sandstones, siltstones and mudstones deposited in a poorly-drained, humid, lowland setting dominated by broad flood plains and lakes (Van Houten 1964; Geolex, accessed 2021), many rich in silica and calcium carbonate (Boles and Surdam 1979). Particularly at its eastern and western ends, the formation is also rich in volcanic detritus from the Yellowstone – Absaroka volcanic field to the northwest, and the Rattlesnake Hills Volcanic Field to the east (Van Houten 1964).

Van Houten (1964) recognized five units within the western region of the Wagon Bed Formation. We could not personally confirm which unit the carpoflora comes from. However, Leopold and MacGinitie (1972: 194) reported

a pollen flora from the "lower part" of the Wagon Bed Formation and stated in the text and associated caption that the fruits and seeds came from the same locality. Love et al. (1978) subsequently stated that this pollen flora came from unit three of Van Houten's system. Leopold and MacGinitie (1972) indicated the pollen flora suggested a Bridgerian age.

Evernden et al. (1964) derived Potassium-Argon dates from units one and three of the western portion of the Wagon Bed Formation. Krishtalka et al. (1987) recalibrated these dates as being 50.3 Ma, or very earliest Bridgerian (earliest middle Eocene), for unit one and 46.6 Ma or latest Bridgerian (late early middle Eocene) for unit three. This accords with the pollen data and with Prothero and Sanchez's (2004) suggestion based on magnetostratigraphy that the upper portion of the Wagon Bed is Uintan (mid-middle Eocene), correlating with chron C20r (43.8–46.2 Ma), and Pekarek et al.'s (1974) report from the eastern Wagon Bed Formation of cross-cutting intrusives recalibrated by Krishtalka et al. (1987) as being at about 45 Ma.

It is apparent that the upper units of the Wagon Bed Formation transition into upper Eocene (Love et al. 1978). Krishtalka et al. (1987) note particularly that Wagon Bed vertebrate fossils recovered from localities along Badwater Creek range from early Bridgerian through late Uintan and into the Duchesnean, thus passing into the late Eocene.

Materials and methods

R. A. Scott obtained nearly 100 specimens of possible plant material preserved as chalcedony casts and permineralizations. Presumably these were collected on the surface as resistant remnants eroded from overlying sediments by deflation. Thirtyeight of these samples were of clear botanical affinity. In some cases internal structure is retained, reflecting infiltration of cellular material by silica, and in at least one case the siliceous exterior protected original organic material on the inside. In most instances, however, it is clear that the silica filled a void or mold, creating a cast without interior detail. In several cases, the translucent silica made it difficult to observe and obtain sharp photographs of surficial details. We therefore coated many of these specimens with palladium in a sputter coater at 12–15 milliamps resulting in a 70 to 90 micron thick coat before photographing with a Canon EOS 450 digital SLR camera and a Nikon SMZ 10 dissecting microscope. To remove the coating the specimens were subsequently soaked in an aqueous solution of sodium cyanide.

Many specimens were also imaged using X-ray microCT scanning, employing a GE Phoenix V|tome|xm240 CT Scanner at the University of Florida College of Engineering Nanoscale Research Facility. Depending on the size of the specimens included in each batch that was scanned, we set the resolution to voxel sizes of 25 to 55 microns, using voltages of 80, 100, and 180 kV, and amperage of 140 to 240 mA, with exposure times of 0.2 to 0.25 seconds. For each session, the container of specimens was rotated through 360 degrees as 1550 to 1800 images were taken. Reconstructed tiff stacks were processed with Volume Graphics Studio Max and Avizo 9.0 lite software to obtain isosurface renderings and virtual slices. Such specimens are indicated by the gold color in the text-figures. Original tif stacks and derived .ply files that can be rotated for three-dimensional viewing, are accessible at Morphosource.org, under the Project heading, "Eocene fruits and seeds, Oil Mountain, Wyoming" (https://www. morphosource.org/projects/000410210). The specimens obtained by R. A. Scott are deposited at the Smithsonian Institution Museum of Natural History, Washington, D.C, with their catalog numbers prefixed USNM. A few additional specimens from the same locality, donated from the estate of Glen and Donna Hood, are deposited at the Denver Museum of Nature and Science, and are prefixed DMNH.

The original collection also includes a variety of additional casts that range from some that are suggestive of a biological origin, gradually grading into structures which, at the other extreme, are clearly abiological concretions. Those forms with characters of apparent biological origin (e.g., surficial cellular structure, a point of attachment, a lineation), but which lack definitive characters allowing further attribution, we here describe as *Carpolithes* Brongn. It is possible that we have included some pseudofossils in these. It is also possible that we missed recognizing others of true biological affinity.

Systematic palaeobotany

Families are arranged in angiosperm phylogeny group order (APG IV 2016), genera and species are in alphabetical order.

Family cf. Pandanaceae R.Br.

Genus indet. aff. *Benstonea* Callm. et Buerki or *Martellidendron* (Pic.Serm.) Callm. et Chassot or *Pandanus* Parkinson s. l.
Text-fig. 1a–f

M a t e r i a l . One specimen, chalcedony cast. USNM PAL 772339.

D e s c r i p t i o n . Endocarp oblong-elongate, in lateral view, 24.6 mm long at its greatest length, slightly trapezoidal in cross section, 15.5 mm by 9.4 mm. Exterior surface marked by low, often discontinuous ridges parallel to the long axis (Text-fig. 1a–c); about 5–6 on the wider faces and 3 on the narrower faces, the ridges incurved at the apex (Text-fig. 1d). Exterior surface marked by impressions of equiaxial cells. Apex flat, eroded, the in-rolled and resistant lip 1.5 to 2 mm wide, surrounding a 4.3 mm deep apical depression, the bottom of this pit with a surface of sand grains (Text-fig. 1e). The base irregular and eroded, surrounded by a 1 mm wide resistant lateral wall which has slightly radially-elongate cells (Text-fig. 1f). The interior space at base is recessed, with a granular matrix, with occasional small ridges and voids. No internal structure was detected in the microCT scans.

D i s c u s s i o n . The Pandanaceae includes five genera and about 700 species of paleotropical shrubs, vines and trees that are particularly widespread in the southwest Pacific but also occur in Madagascar and eastern Africa (Buerki et al. 2012, Callmander et al. 2012). While many taxa are littoral, others occur in montane settings and, appropriate to the Wagon Bed, river margins (Dahlgren et al. 1985, Stone

et al. 1998). The fruits are berries (*Freycinetia* GAUDICH., *Sararanga* HEMSL.) or drupes (*Pandanus*, *Martellidendron*, *Benstonea*) borne in globose heads. The ovary is superior and may bear 1–12 carpels (Mabberley 2008). Within the drupaceous forms, individual units can involve either a single fruit or several fruits fused into "polydrupes" (Stone et al. 1998, Callmander et al. 2003, 2012). Often the mesocarp of the drupe forms a fleshy extension, distal to the endocarp, and sometimes (*Benstonea*) separated from it by a thin partition (Callmander et al. 2012). Germination occurs through the base of the drupe.

The fossil accords in its morphology to a single drupe, similar to individual drupes of *Pandanus* s. l. in its overall form. The apical depression could reflect the missing apical mesocarp. The rhomboidal shape of the fossil suggests the influence of adjacent drupes in the larger infructescence. The distinction between *Martellidendron* and *Pandanus* + *Benstonea* is that, in the former, the endocarp does not extend between the seed locules, but is replaced by the mesocarp, which extends from the apex to the base, while in the latter the endocarp extends between the seed locules and is surrounded by the mesocarp (Callmander et al. 2012). In the specimen at hand, the inferred endocarp wall does not appear to possess extensions into the central cavity, suggesting affinity with *Martellildendron*. This would be consonant with the ages of divergence deduced by Gallaher et al. (2015), based upon molecular data, who suggest that *Pandanus* and *Benstonea* diverged in the later Oligocene to Miocene, but that the split between *Martellidendron* and the common ancestor of *Pandanus* + *Benstonea* might have occurred as early as the late Eocene. However, the fossil as currently understood does not provide evidence of being bilocular, a character defining *Martellildendron* (Callmander et al. 2003). Further, while the overall morphology is strongly suggestive of Pandanaceae, the fossil lacks the diagnostic apical pileus and stigmas that would confirm this assignment (pers. com. M. Callmander, June 2021). Thus, we suggest that the fossil belongs to the Pandanaceae, and potentially to the *Martellidendron* + (*Pandanus* + *Benstonia*) clade but cannot provide a more certain attribution.

An Eocene *Pandanus* in Wyoming would not be without precedent. Dorf (1938) described and illustrated a leaf as *Pandanites corsonii* DORF from the Late Cretaceous Medicine Bow Formation of southeastern Wyoming. Upchurch and Mack (1998) also reported (without illustration) a leaf of *Pandanites* from the Maastrichtian of New Mexico. While these North American reports have not been re-evaluated, Kvaček and Herman (2004) reported a leaf of *Pandanites trinervis* (ETTINGSH.) J.KVAČEK et A.B.HERMAN from the early Campanian of Austria and the Maastrichtian of Romania based on both morphological and cuticular data, indicating the presence of a *Pandanus*-like plant in the Northern Hemisphere in the Late Cretaceous. In their article they state that "It is difficult to find significant differences between" the European *P. trinervis* and Dorf's specimen. Pollen referred to

Pandaniidites ELSIK has been reported from North America, with the oldest accepted (Muller 1981) pollen being from the Maastrichtian of Canada (Jarzen 1978, see also Elsik 1968, Leffingwell 1971, Jarzen 1983). However, Stockey et al. (1997a) noted that this pollen has a strong similarity to that found *in situ* in flowers of *Limnobiophyllum* KRASSILOV, an extinct member of the Lemnoid Araceae (see also, Hotton et al. 1994). Hence the pollen evidence for Pandanaceae remains equivocal.

Family Menispermaceae JUSS.

Genus *Chandlera* R.A.SCOTT

### *Chandlera lacunosa* R.A.SCOTT
Text-fig. 1g–n

M a t e r i a l . One specimen, USNM PAL 772340, preserved in translucent chalcedony.

D e s c r i p t i o n . Endocarp lozenge-like, elongate-elliptic in face view (Text-fig. 1g–h), narrowly elongate-elliptic in lateral view (Text-fig. 1i) with long, slightly convex, sides; narrowly elliptic in cross section (Text-fig. 1k–n). 37 mm long, 18 mm wide and 12.5 mm thick; bilaterally symmetrical; the plane of symmetry running longitudinally, bisecting the width. Surface of endocarp smooth, with a very faint median longitudinal lineation. In cross section, a central reniform locule 7.5 mm wide by 3 mm high is present, surrounded by 6 smaller cavities on the dorsal and lateral flanks, ranging from nearly circular to more elliptic (2 × 2.5 mm to 3 × 4.5 mm), separated by 1–2 mm thick walls (Text-fig. 1j, n). The endocarp wall is 3–4 mm thick. The translucent dorsal surface reveals that the endocarp cavities are longitudinally elongate, dorsal and lateral to the locule, and are linked in a network via transverse cross-cavities (Text-fig. 1g, j). The ventral side of the endocarp, below the central locule, is infilled by chalcedony with only a hint of a pair of cavities. Both the apical and basal ends of the endocarp are marked by paired, round to elliptical concavities, separated by a median wall and an overhanging dorsal beak (Text-fig. 1k–m). These concavities, or apertures, measure 3 × 5 mm at the apical end and 2.5 × 2.5 mm at the base. The apertures link to the network of elongate and cross cavities within the endocarp wall. Some of the cavities are filled with sand and clay while others remain empty (Text-fig. 1m). No cellular structure is discernable.

D i s c u s s i o n . This fossil conforms closely to *Chandlera lacunosa* (tribe Tinosporeae, Menispermaceae) first described by Scott (1954, 1956) and further detailed by Manchester (1994) from the middle Eocene Clarno flora of Oregon. The single specimen falls approximately in the middle of the size range of the Clarno specimens. We illustrate examples of well-preserved specimens from the Clarno Nut Beds for comparison (Text-fig. 1o–r). The convex surface

Text-fig. 1. cf. Pandanaceae (a–f), Menispermaceae (g–r). a–f: cf. Pandanaceae genus indet. Chalcedony cast of possible fruit segment, USNM PAL 772339. a: Lateral view, reflected light, palladium coated. b–f: Micro-CT scan surface renderings. b, c: Lateral views illustrating striations, d: Median longitudinal digital section showing the pronounced concavity at apex and indentation at base. e: Apical view, with inrolled margin. f: Basal view. g–n: *Chandlera lacunosa*, Wagon Bed. Silica cast of endocarp, USNM PAL 772340.
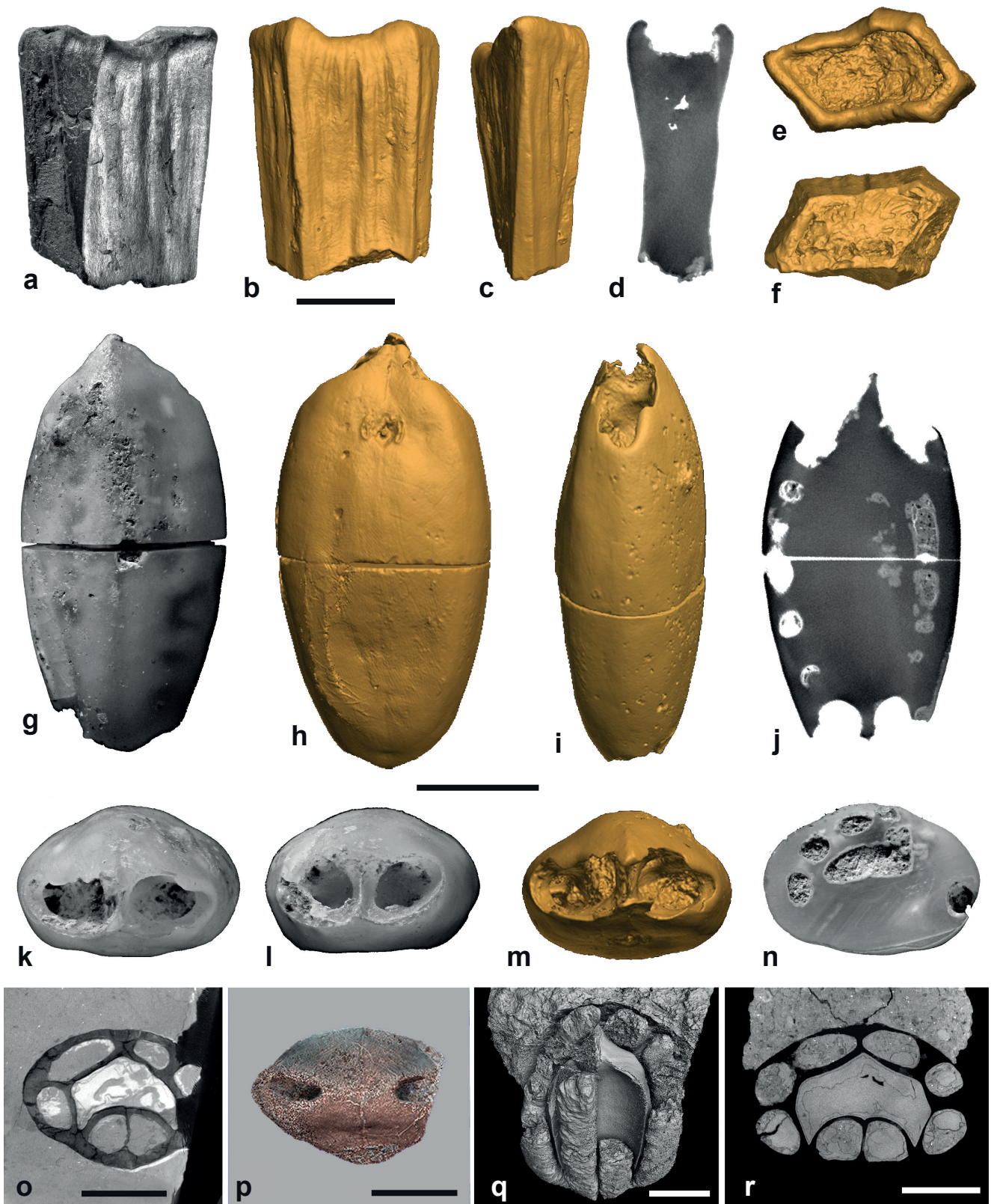
g: Ventral view of semi-translucent endocarp, with faint silhouette of interconnected lacunae, reflected and transmitted light, uncoated. h, i: Dorsal and lateral views, micro-CT scan surface rendering. j: Virtual median longitudinal section in dorsi-ventral plane intercepting rows of lacunae within the endocarp wall. k: Apical, l: basal views, reflected light. m: Apical view, cf. (k), micro-CT scan surface rendering. n: Physical transverse section in the plane of saw cut seen in (g–j), reflected light. Note remains of curved locule in center and surrounding lacunae. o–r: *Chandlera lacunosa* from the type locality in the Clarno Formation of Oregon for comparison, surface and sectional views from micro-CT scanning. o: Transverse section showing central locule surrounded by endocarp with prominent lacunae, including a pair of ventral lacunae adjacent to the concave surface of the locule, UF225-33628. p: Same specimen, surface rendering of the basal end with prominent pair of apertures and median groove. q: Oblique-ventral view of specimen fractured to show boat-shaped locule cast surrounded by fragmentary remains of the endocarp, UF225-6849. r: Same specimen in virtual transverse section, showing lacunae surrounding the locule in arrangement similar to that of (n). Scale bars = 1 cm. Bar at (b) applies to (a–f); bar at (i) applies to (g–n).

of the locule coincides with the endocarp dorsal surface. The presence of apical and basal paired apertures (Text-fig. 1k–m) leading to six reticulated, dorsal-lateral, channels in the endocarp (Text-fig. 1j) matches the condition in the Clarno specimens (Text-fig. 1p, q). A physical transverse section of the Wagon Bed specimen intercepted some of these channels (Text-fig. 1n), which are also seen in X-ray imagery, for example in virtual longitudinal section (Text-fig. 1i). However, the Wagon Bed specimen does not clearly show the two ventral (condylar) lacunae seen in the Clarno specimens (Text-fig. 1o, r). We interpret this as an artifact of preservation whereby chalcedony entered the basal and/or apical apertures and infilled these lacunae after the endocarp wall had disintegrated and been infilled with chalcedony forming the initial cast. A very faint medial hairline groove on the ventral surface (text-fig. 1h) resembles the median longitudinal line seen in the Clarno specimens (Text-fig. 1p; Manchester 1994). The locule is not fully preserved, but appears to conform to the flattened, boat shaped, locule of *Chandlera* R.A.Scott (Text-fig. 1q). The absence of cellular detail precludes further anatomical interpretation.

This is the first report of *Chandlera* beyond the Clarno Formation, extending its range to the Rocky Mountains in the middle Eocene. Endocarps of Menispermaceae are common in the Eocene of the Northern Hemisphere, and are generically diverse in the Clarno (Manchester 1994), London Clay (Chandler 1961), Messel (Collinson et al. 2012) and Le Quesnoy (Jacques and De Franceschi 2005) floras, among others. Today, the Tinosporeae are the most diverse tribe of the family and are pantropical with more temperate outliers (Kessler 1993). Extant genera are readily distinguishable from each other on the basis of fruit morphology (e.g., Jacques 2009). Within the Tinosporeae, Scott (1954, 1956) suggested that extant *Parabaena* Miers, a climbing vine of Indomalaysia, possessed the most similar living endocarp, although they differ greatly in size and sculpture (Scott 1956, Jacques 2009). It is noteworthy that the family is dominated by vines and climbing shrubs, suggesting that the vegetation at the Wagon Bed locality offered a sufficiently forested environment for lianas.

Family Salicaceae Mirb.

Genus *Saxifragispermum* E.Reid et M.Chandler
Text-fig. 2a–g

M a t e r i a l . One specimen, silicified exterior with original internal organic material. USNM PAL 772341.

D e s c r i p t i o n . A loculicidal capsule, narrowly ovate to ovate in side view (Text-fig. 2a, b), rounded/four angled in cross section (Text-fig. 2c–d), 10.2 mm long and 4.1 × 4.9 mm in width. The four angles each with a central linear groove suggestive of a plane of weakness (Text-fig. 2a, b). The grooves meet at the pointed apex and converge on an inflated and protruding point of attachment at the base. The grooves circumscribe four valves that are evenly pitted on their surface. An equatorial transverse cut revealed a geode lined by quartz crystals, lacking preservation of wall structure and placentae, but with central cavity filled with ovoid structures resembling seeds within a tangle of soft, whitish threads interpreted as trichomes or fibers (Text-fig. 2e–g).

D i s c u s s i o n . This specimen resembles, in its exterior form, the fruits of *Saxifragispermum spinosissimum* E.Reid et M.Chandler, previously described from the London Clay flora (Reid and Chandler 1933, Chandler 1961), and *S. tetragonalis* Manchester from the Clarno flora (Manchester 1994). While the specimens from those sites are permineralized and preserve the cellular structure of the fruit, the Wagon Bed specimen is a cast with a hollow center. Cutting the specimen transversely in half revealed a peripheral lining of quartz crystals and a central unmineralized cavity filled with apparent original material including a matrix of thin whitish threads that might be trichomes or fibers, surrounding brown ellipsoidal structures resembling seeds (Text-fig. 2e, f). Despite the implications of the generic name *Saxifragispermum* as assigned by Reid and Chandler (1933), it was subsequently allied with the Flacourtiaceae DC. (Chandler 1961, Manchester 1994) which has been subsumed in the Salicaceae (Boucher et al. 2003). Assignment of the Wagon Bed specimen to this family cannot be absolutely confirmed because the distinctive parietal placentation seen in the London Clay and Clarno specimens is not preserved. However, the overall morphology of the fruit (four-valved, angled capsule, coupled with seeds embedded in a fibrous matrix) closely resembles that of the London Clay and Clarno taxa, although the Wagon Bed specimen is closer in size to the Clarno species.

The thread-like locule filling of this specimen, like that of the Clarno and London Clay specimens, is suggestive of the tightly packed plumed seeds of extant *Salix* L. and *Populus* L. fruits. The Wagon Bed occurrence extends the North American range of the genus to the Rocky Mountains. In the Green River Formation, Salicaceae are represented by compressed fruit capsules as well as leaves of *Populus* (Manchester et al. 2006) and *Pseudosalix* L.Boucher, Manchester et Judd (Boucher et al. 2003). Although it is difficult to make a detailed comparison because of the different modes of preservation, there is a noteworthy similarity between *Saxifragispermum* and the capsules of *Populus tidwellii* Manchester et Judd from Utah and *P. cinnamomoides* (Lesq.) MacGinitie from Wyoming as illustrated in Manchester et al. (2006: e.g., figs 5e, f, 6g–k).

Family Cannabaceae Martinov (Celtidaceae Endl.)

Genus *Celtis* L.
Text-fig. 2h–j

M a t e r i a l . Two specimens, silicified. USNM PAL 772342, DMNH EPI.47809.

D e s c r i p t i o n . Endocarp elliptic in lateral view, nearly round in cross section, USNM PAL 772342 – 11 mm long and 8.5 mm wide in the plane of symmetry and 8 mm perpendicular to it (Text-fig. 2h–j); DMNH EPI.47809 – 8.8 mm long and 7.4 mm wide in the plane of symmetry and 7.0 mm perpendicular to it. Apex somewhat acute with a point, base rounded with an indistinct pit of attachment. The endocarp marked by a fine groove in the plane of symmetry (Text-fig. 2j), extending from the apex to the base, dividing the endocarp into two symmetrical halves. Endocarp surface marked by depressions approximately 0.75 mm in diameter, these running in poorly-defined longitudinal rows of 8 to

9 pits each (Text-fig. 2h, j). The inter-depression areas marked by ridges that have uneven high points which create a series of tubercles between the depressions. Endocarp abraded, and no evidence of cellular structure is exhibited on the surface.

D i s c u s s i o n . The Wagon Bed specimens conform to the morphology of the endocarps of *Celtis*, a common fossil of western North America and of Europe (Manchester 1989). *Celtis phenacodorum* (Cockerell) E.W.Berry often co-occurs with vertebrate material in the early Eocene of Wyoming, first appearing in late Clarkforkian assemblages and becoming widespread in Wasatchian time (Gingerich 1989). Samples of *C. phenacodorum* from western Polecat Bench, Wyoming, illustrated in Manchester et al. (2002: pl. 4, figs O–S) are virtually identical in morphology to the Wagon Bed specimen, except in two respects. First, while the Wagon Bed specimens exhibit a clear lineation on the side of the endocarp in the plane of suture, it appears to lack a secondary keel situated at right angles to the plane of suture. However, as noted above, the surface is abraded, and in Manchester et al. (2002: pl. 4, figs O–S) the minor keel is not particularly apparent. Second, at 11 mm and 8.8 mm in length, the Wagon Bed specimens are somewhat larger than the Paleocene specimens illustrated in Manchester et al. (2002) which average ~8.5 mm long, or the early Eocene ones described by Gingerich (1989) which average 5 mm in length. They are also substantially larger than the *Celtis* from the middle Eocene Clarno flora (average length 4.7 mm). Gingerich (1989) notes that *Celtis* endocarps commonly occur with vertebrate material, and suggests that their preservation is favored by calcium-rich environments. Modern *Celtis* is a genus of trees and shrubs that are widespread in temperate and tropical environments of both hemispheres. While most of the endocarps reported in the fossil record are less than a cm in diameter, some of the living tropical species (e.g., *C. phillipinensis* Blanco) have large endocarps similar to the size of this fossil (e.g., Sattarian and van der Maesen 2006).

Family Cannabaceae Martinov (Ulmaceae II)

Genus *Aphananthe* Planch.
Text-fig. 2k–n

M a t e r i a l . One specimen, chalcedony cast. USNM PAL 772344.

D e s c r i p t i o n . Endocarp elliptical in lateral view and triangular in cross section, 8.3 mm long, 5.5 mm wide on the major axis and 4.7 mm wide on the minor axis (Text-fig. 2k–m). Apex marked by a small protrusion or placental plug. Three raised ridges radiate from the apex, creating the three angles of the endocarp (Text-fig. 2k). Base rounded. Much of the surface is very finely papillate, possibly reflecting the surficial cell structure (Text-fig. 2n). No details of the endocarp wall structure are preserved.

D i s c u s s i o n . The specimen conforms in endocarp morphology with extant species of *Aphananthe* documented by Manchester (1989) and accords with *Aphananthe maii* Manchester of the middle Eocene Clarno flora of Oregon in all characters that are preserved. The coiled embryo seen in the Clarno material (Manchester 1994) and in extant species is not preserved in this specimen, nor in the similar unnamed species from the late Eocene of Oregon (Manchester and McIntosh 2007). As with *Chandlera*, the Wagon Bed flora provides a Rocky Mountain occurrence of the genus in the North American Paleogene record. It is also reported in the Oligocene of western Siberia (Dorofeev 1982) and the Holocene of Japan (Miki 1938). The modern genus includes five species of deciduous or semi-deciduous shrubs or trees, three widely distributed from Japan to India and south to Australia, one in Madagascar and one in Mexico (Todzia 1993, Mabberley 2008).

Family Betulaceae Gray

Genus *Coryloides* Manchester
Text-fig. 2o–r

M a t e r i a l . One specimen, chalcedony cast. USNM PAL 772345.

D e s c r i p t i o n . Distorted sphere, 20.5 mm high, 18.9 mm on one equatorial axis, 21.7 mm on the opposite axis. One end surmounted by a very clearly demarcated disk, 11 × 12.5 mm in diameter, distorted on the same axes as the larger specimen. The center of the disk is smoother than the surface of the sphere as a whole, and tapers to a conical point (Text-fig. 2o–q). There is a suggestion that the surface of the sphere laps up against the margin of the terminal disk in one or more layers, the innermost exhibiting an undulating margin (Text-fig. 2p). The surface of the rest of the sphere is unevenly rumpled, and is traversed by eight faint, equidistant, longitudinal striations.

D i s c u s s i o n . We interpret this fossil as a locule cast or seed of *Coryloides* Manchester, first described from the Clarno flora (Manchester 1994). Initially we thought that this was the exterior of a poorly preserved fruit of some form. However, at least one Clarno specimen of *Coryloides* (pl. 7, fig. 12 in Manchester 1994) exhibits a broken nut, exposing a contained locule cast or seed. Re-examination of this latter specimen reveals that the locule cast/seed exhibits a large, circular, scar with a central pointed tip. This scar is not aligned with the basal cupule scar of the fruit (Manchester 1994: pl. 7, figs 7, 9, 10). It is unclear from present data if this scar and point represents the micropylar end of the seed, or more plausibly due to its complexity, the chalaza.

The unevenly distorted surface of the Wagon Bed specimen suggests that the living structure had a flexible surface with a degree of plasticity that could be easily deformed in the preservational process; if the fossil represents a seed, it could well have been deformed in preservation, much as the specimen in pl. 7, fig. 12 of Manchester (1994). The surface of the Wagon Bed specimen is traversed by widely spaced, equidistant, longitudinal grooves. As with other Wagon Bed taxa, the presence of *Coryloides* suggests a geographic link with the Clarno flora.

Although the external surface of *Coryloides* nuts resembles that of extant *Corylus* L. in the Betulaceae, the locule morphology as seen in the Nut Beds and Wagon Bed specimens does not match that of the extant genus; whether this reflects true relationship or a convergent morphology within the Betulaceae (Manchester 1994) is unclear. *Corylus* is currently represented by about 18 species of deciduous trees and shrubs of the Northern Hemisphere (Mabberly 2008).
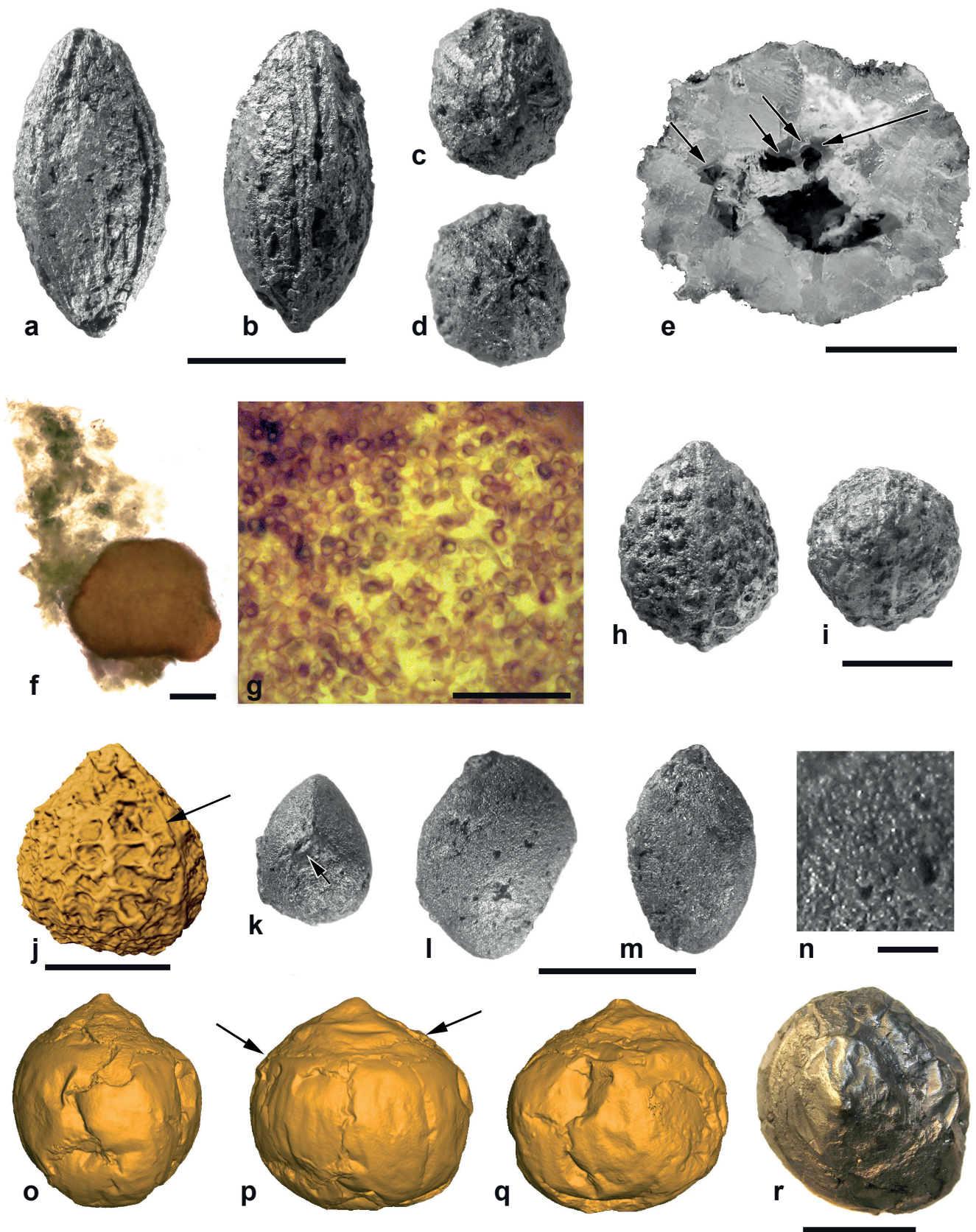
Text-fig. 2. Salicaceae (a–g), Cannabaceae (h–n), cf. Betulaceae (o–r). a–g: *Saxifragispermum*, USNM PAL 772341. Scale bar = 5 mm except as indicated. a–b: Lateral, c: apical, and d: basal views of fruit, reflected light, palladium coated; apex at top of (a, b). e: Equatorial transverse section reflected light; arrows indicate presumed seeds, scale bar = 2 mm. f: Detail of locule contents extracted from (e), transmitted light, scale bar = 200 μm. g: Interwoven trichomes or fibers from locule, transmitted light, scale bar = 5 μm. h–j: *Celtis*. h, i: USNM PAL 772342, reflected light, palladium coated, scale bar = 5 mm. h: Lateral view parallel with plane of dehiscence. i: Lateral view perpendicular to plane of dehiscence. j: DMNH EPI.47809, *Celtis* in lateral view; showing reticulate sculpture and the vertically-oriented, plane of dehiscence (arrow), scale bar = 5 mm. k–m: *Aphananthe*. USNM PAL 772344, reflected light, palladium coated, scale bar = 5 mm. k: Apical view, note triangular cross section and apical plug (arrow). l: Lateral view, apex up. m: Lateral view at 90° to (l). n: Detail of cellular pattern at surface of endocarp, scale bar = 0.5 mm. o–r:

Family Juglandaceae DC. ex Perleb

Genus *Carya* Nutt.
Text-figs 3a–x, 4a–w

M a t e r i a l . Ten specimens, four whole, three half nuts and three more fragmentary. Many chalcedony casts. Three specimens exhibiting casts of the seed, one specimen permineralized and displaying some internal structure. USNM PAL 772346, 772347, 772348, 772350, 772351, 772352, 772353, 772354, 772355, 772356.

D e s c r i p t i o n . Nuts ovoid in side view, almost circular in cross section, but with a sense of a four angled symmetry (e.g., Text-fig. 3c), unilocular, with a single seed. Of the eight reasonably complete full or half nuts the average height is 27.2 mm (range 23.7 to 30.5 mm), the diameter parallel to plane of dehiscence average 22.6 mm (range 19.5 to 27 mm), and the diameter perpendicular to plane of dehiscence average 22.5 mm (range 19.1 to 28.4 mm). Surface smooth, often marked by eight very fine longitudinal grooves (Text-fig. 4b, c, u). Base generally rounded, although in some cases with a slight protrusion. Lateral walls 3–4 mm thick, possibly thickening towards the base. Primary septum (perpendicular to plane of dehiscence) 2 to as much as 5 mm wide at base, tapering to 1 to 2 mm at apex, and extending ~3/4 of the distance to the top of the locule (Text-figs 3e, m, n, s, t, x, 4g, h, p, q, v, w). A pair of placental vascular bundles arises at the base of the primary septum, but these bundles soon diverge (e.g., Text-fig. 3l, n, v), each arching close to the periphery of the primary septum, rather than running parallel to the nut axis. Secondary septum present near base of the nut, and, along with the primary septum, dividing the base of the locule into four lobes (Text-figs 3n, x, 4k); secondary septum shorter and narrower than the primary septum. Interior of locule smooth with no inner ribs. Locule narrower in the plane of the primary septum (10 mm) than perpendicular to it (14 mm). Two narrow, continuous, lacunae present in the wall of the nut, originating approximately 1/4 of the way from the base of the fruit and extending to near the apex; possibly bifurcated at the base, but coalescing into a single arcuate cavity in each half of the nutshell, enveloping the locule towards the apex (Text-figs 3j, k, m, 4i, j). Cellular structure present in one specimen, where a cross-section reveals the core of the nut to be composed of equiaxial cells. In others, the exterior displays radiating structure that might represent radially-elongate mineral fibers (Text-figs 3i, j, 4q). Seed elongate, 12 mm wide × 17 mm high with a convex shoulder region (Text-fig. 4f, h, l); seed coat thin (Text-fig. 4j) and apparently papery.

D i s c u s s i o n . The fossils are clearly nuts of the Juglandaceae, with a resemblance to both *Juglans* L. and *Carya*. Some specimens appear to be isolated nuts without preservation of the surrounding husk, but in others the nutshell is permineralized and appears dark in reflected light, and is surrounded by a distinct, but less well preserved

lighter colored layer that may represent the husk (as seen in Text-fig. 3i–m, u, v). Scott (1954), Leroy (1955), Manchester (1987) and Manchester and McIntosh (2007) provide characters to distinguish these two genera. While the mode of preservation impedes determination of some of these characters (e.g., dehiscence of the husk, complete path of placental bundles within the nut), others can be evaluated. Our discussion below progresses from characters that suggest affinity with *Carya* to those that are less decisive.

The smooth surface seen in the fossils is more commonly characteristic of *Carya* than *Juglans*, although it can occur in some modern species of the latter. There is a hint of a protuberant base in three of the Wagon Bed fossils similar to the condition in *Carya* (Manchester 1987). The position of the pair of placentary bundles, whether running parallel and adjacent to the central axis as in *Juglans*, or diverging from one another near the base and following a peripheral course before converging toward the seed apex as in *Carya*, is an important distinguishing feature (Leroy 1955), but the configuration is not well preserved in most of these specimens. However, by moving through virtual slices of the two permineralized specimens shown in Text-fig. 3j–n and s–x, we were able to follow the faint traces of these bundles. Although the bundles are closely adjacent at the base of the nut (Text-fig. 3n), longitudinal sections in plane of the primary septum (Text-fig. 3l) show that they quickly diverge and assume a peripheral course in the manner of *Carya*. The seed has a rounded shoulder, is axially elongate within the locule, and is distinctly narrower in plane of primary septum and wider perpendicular to it (Text-fig. 4l), all characteristic of *Carya* (Manchester 1987, Manchester and McIntosh 2007). The available characters of the Wagon Bed specimens conform more closely to *Carya* than to *Juglans* and are reminiscent of the specimens from Post, Oregon (Manchester and McIntosh 2007) and the European Cenozoic (Mai 1981). These represent one of the oldest occurrences of *Carya* nuts, the next oldest being those from the late Eocene of Oregon (Manchester and McIntosh 2007) and Neogene of Europe (Mai 1981). *Carya* is also represented by pollen in the Wagon Bed flora (Leopold and MacGinitie 1972). In the current day, *Carya* comprises some 18–24 species of temperate trees, distributed in North and Central America, with a lesser diversity in eastern Asia (Mabberley 2008).

Turning to those characters that are less indicative of *Carya*, the presence of inner ribs perpendicular to the median septum is characteristic of *Carya* (Manchester 1987). These are missing in the fossil, although fig. 3, 1 in Manchester (1987) suggests these may be very subdued in some cases. This is also true of some living species, e.g., in extant *Carya poilanei* (A. Chev.) J.-F. Leroy of Vietnam and Southern China (Mai 1981, Zhang et al. 2022). The nuts of *Carya* possess a four-angled amb (Manchester 1987), a character only mildly expressed in two of the ten fossils presented here (Text-figs 3c, 4b), although many are casts with some

Coryloides locule cast, USNM PAL 772345, scale bar = 1 cm. o: Lateral view illustrating a disk-like structure at top surmounted by a central point, and the rumpled appearance of the surface, suggesting a possibly flexible texture. p: Lateral view rotated 90°, disk up, the separation between the pointed disk and the rest of the fossil distinct (arrows). q: Lateral view rotated 180° from (p). r: Apical view with circular disk and central point. p–q: Micro-CT scan surface rendering. r: Reflected light, palladium coated.
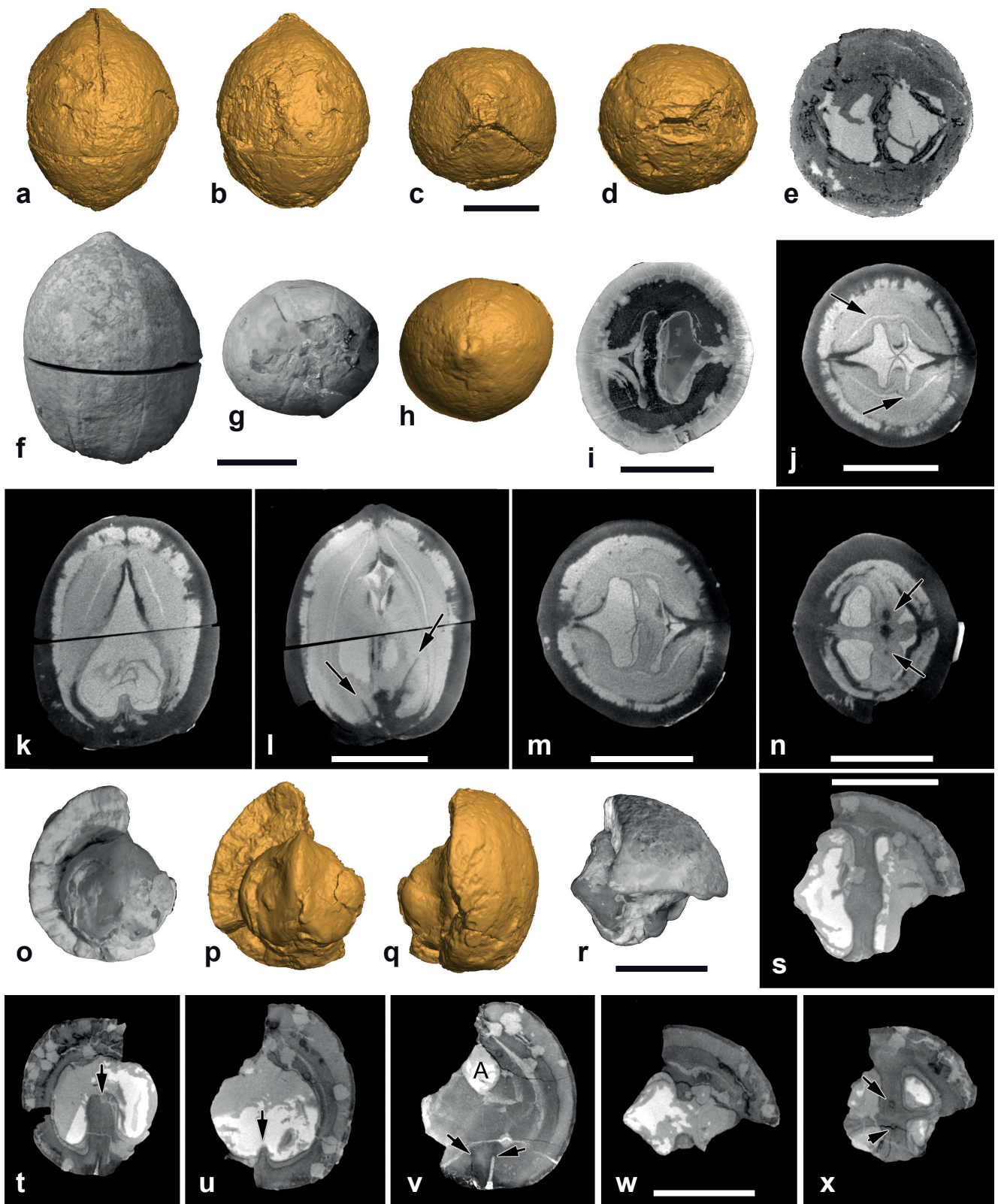
Text-fig. 3. Juglandaceae. *Carya* (a–x). Scale bars = 1 cm. a–e: USNM PAL 772346. Micro-CT scan surface rendering. a, b: Lateral, c: apical, d: basal views. e: Virtual equatorial transverse section. f–n: USNM PAL 772347. f: Lateral view, reflected light, showing path of saw cut for transverse section of (i). g: Basal view, reflected light. h: Apical view, micro-CT surface rendering. i: Physical transverse section displaying locule and cellular preservation of parts of wall. j–n: Virtual sections from micro-CT scan data. j: Transverse section at apical 1/3 of nut. Note narrow lacunae (arrows). k: Longitudinal section parallel to primary septum, traversing one of the cotyledon lobes and showing secondary septum at base. l: Longitudinal section in plane at right angles to (k) in plane of primary septum, showing divergent placental bundles arising from base of nut (arrows). m: Equatorial transverse section showing two lobes of locule separated by primary septum. n: Transverse section near base of nut showing primary and secondary septa, creating four basal lobes of locule; note diverging placental bundles (arrows). o–x: USNM PAL 772351. o: Lateral view of broken nut with exposed locule cast, reflected light. p: Same orientation of nut, micro-CT surface rendering. q: Same specimen lateral view, rotated 90° from (p), micro-CT surface rendering. r: Apical view, reflected light. s–x: Virtual sections from micro-CT

distortion of the exterior surface. Nuts of *Juglans* generally possess prominent multilobed lacunae in their walls; lacunae are lacking in many species of *Carya* except in sections *Apocarya* and *Sinocarya* (Manchester 1987) which possess simple lacunae. Narrow lacunae are readily observed in the permineralized Wagon Bed specimens (e.g., Text figs 3e, j–m, 4i, j), and are present in specimens of *Carya* from the late Eocene of Oregon (Manchester and McIntosh 2007).

Family Anacardiaceae R.Br.
Tribe Spondioideae Takht.

Genus cf. *Pentoperculum* (E.Reid et M.Chandler) Manchester
Text-fig. 5a–f

M a t e r i a l . Three specimens USNM PAL. 772349, 772359, 772360.

D e s c r i p t i o n . Endocarp broadly ovate in lateral view, the lower half shallowly dish-shaped (Text-fig. 5a), the upper portion an inverted bowl containing six locules. Round to polygonal in cross section, the polygon reflecting the number of locules (Text-fig. 5b, c). USNM 772359 height 11.8 mm, width 13.9 mm × 14.2 mm; USNM 772360 height 12 mm, width 14 mm × 14.5 mm, USNM PAL 772349 height 8.8 mm, width 11.0 × 11.8 mm. The base slightly rounded to flat, bearing a circular pit of attachment ca. 1 mm in diameter (Text-fig. 5c). In each specimen the ridges radiate from the basal scar to the equator of the endocarp, terminating opposite the base of the locules, the ridges thus as many in number as locules. In USNM 772359 there are twice as many ridges, the ridges both opposite and alternating with the locules. The apex rounded, often eroded, with six axially-elongate valves that average 6.4 mm long (range 5.8–6.9 mm) and 3.7 mm wide (range 3.4–3.9 mm). These valves are bipartite, the center marked by a longitudinal groove (Text-fig. 5a, d). No internal anatomy is discernible, and there are no apparent depressions on the surface.

D i s c u s s i o n . The structure of these multi-carpellate, operculate endocarps clearly allies them with the subfamily Spondioideae of the Anacardiaceae (Wannan and Quinn 1990, Mitchell et al. 2006, Herrera et al. 2018). Among living genera, the possession of 6 carpels is more like extant *Pleiogynium* Engl. which exhibits 5–12 carpels, than the remaining genera of Spondioideae, which possess from one to, at most, 5, mature carpels. However, *Pleiogynium* lacks bipartite opercula. Two living genera (*Haematostaphis* Hook.f., *Pseudospondias* Engl.) and the extinct *Pentoperculum* Manchester exhibit bipartite opercula (Hill 1933, 1937, Herrera et al. 2018), whereas unitary opercula are noted in other genera, e.g., *Antrocaryon* Pierre, *Dracontomelon* Blume and *Sclerocarya* Hochst. The fruit morphology of all extant genera of Spondioideae was reviewed by Herrera et al (2018).

Reid and Chandler (1933) noted the presence of basal or sub-equatorial pores that link with lacunae in the endocarp wall of several living species of *Dracontomelon*, features observed by other authors (e.g., Hill 1933, Chesters 1957, Tardieu-Blot 1962, Wilkinson 1968). These characters, seen also in the Clarno specimens of *Pentoperculum*, are not present in the Wagon Bed fossils – possibly because of the limited detail preserved in these casts.

On the basis of the available characters, these Wagon Bed fossils cannot be clearly allied with any extant genus. These fossils are similar in many respects to *Pentoperculum minimum* (E.Reid et M.Chandler) Manchester (Manchester 1994) from the early Eocene London Clay and middle Eocene Clarno Formation in general appearance, and the possession of bipartite opercula. Although that genus usually has five locules, occasional 4- and 6-locular specimens were also observed (Manchester 1994). However, the Wagon Bed specimens lack internal detail and are about twice the size of those from Clarno. A second *Pentoperculum* species from London Clay, "*Dracontomelon*" *subglobosum* E.Reid et M.Chandler (Manchester and Collinson, in progress), has larger endocarps similar in size to the Wagon Bed fossils, but possesses 5 locules.

Tribe Spondioideae Takht.

Genus cf. *Pleiogynium* Engl.
Text-fig. 5j–m

M a t e r i a l . One fruit replaced by chalcedony, USNM PAL 772357.

D e s c r i p t i o n . Endocarp subglobose, but wider below the equator than above (Text-fig. 5j, k), rounded-elliptical in transverse view, height 16 mm, diameter 15.5 × 18.4 mm. The base slightly rounded to flat, bearing a circular pit of attachment ca. 1 mm in diameter (Text-fig. 5m). The apical surface smoothly rounded. Nine locules, each with an elliptical germination aperture; germination apertures in a cycle extending from the equator toward the fruit apex (Text-fig. 5j, k). One locule (Text-fig. 5j, left side) covered by a bulging surface 5.2 mm high by 3.9 mm wide, with no sign of being bipartite. Locules possessing a bipartite inner lining (Text-fig. 5k). Ridges radiate from the basal scar to the equator of the endocarp, aligned with the locules.

D i s c u s s i o n . This is the largest of the Spondioid fruits from the Wagon Bed flora and possesses 9 locules (Text-fig. 5l). In the high number of locules, the fruit resembles extant *Pleiogynium*, which is distinguished from other genera of the Spondioideae that are typically 1- to 5-locular. Eight of the exposed locules on this specimen have open apertures, but one is covered with a bulging surface. Although rounded opercula are characteristic of some extant Spondioid genera, such *Poupartia* Comm. ex Juss., *Antrocaryon*, etc., *Pleiogynium* locules lack opercula (Rozefelds et al. 2015, Herrera et

scans. s: Equatorial transverse section. t: Longitudinal section perpendicular to primary septum, note thick primary septum (arrow). u: Longitudinal section parallel to primary septum transecting one of the cotyledons; note narrow secondary septum at base (arrow). v: Longitudinal section in plane of the primary septum; note apical aperture (A) connecting the two main lobes of the locule and divergent pair of placental bundles arising from base (arrows). w: Transverse section in apical 1/3 of nut showing the connection between the two main lobes of the locule via the aperture seen in (v). x: Transverse section of the base of the nut showing the four lobes of the locule separated by the primary and secondary septa. Note placental bundles in primary septum (arrows).
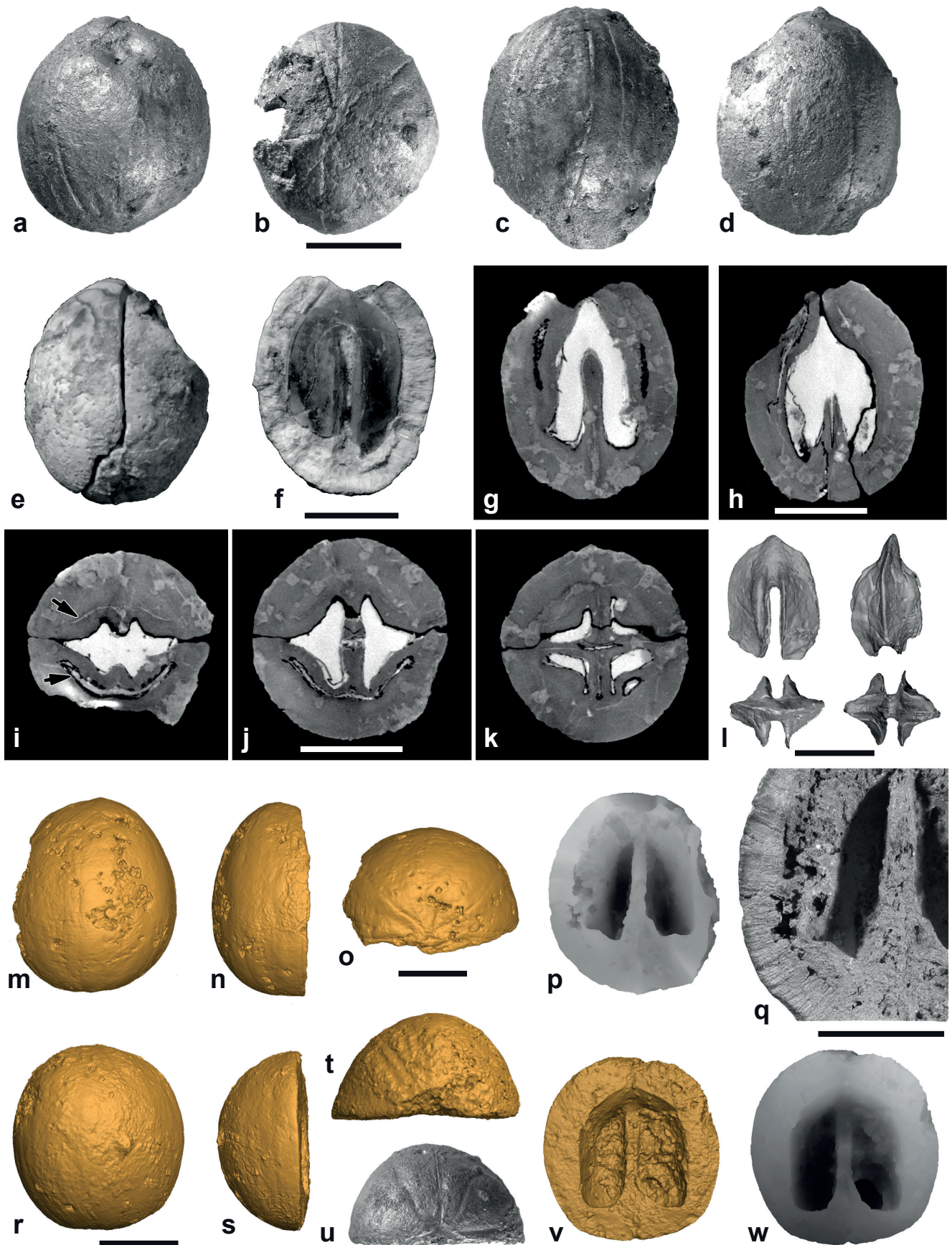
Text-fig. 4. Juglandaceae *Carya* (a–w). Scale bars = 1 cm. a–d: USNM PAL 772352, reflected light, palladium coated. a: Oblique-lateral view of nut, apex up. b: Basal view with damage to left and clear depiction of meridional grooves. c, d: Two lateral views oriented about 130° from each other and avoiding the area of damage; the meridional grooves clear in (c). e–l: USNM PAL 772350. e: Intact nut, lateral view, apex up, reflected light. f: One half of split nut revealing in situ chalcedony locule cast, reflected light. g–k: Virtual sections from micro-CT data. g: Longitudinal section parallel to the exposed face in (f). h: Longitudinal section at 90° from (g). i: Transverse section in apical 1/3 showing locule bracketed by C-shaped lacunae (arrows). j: Equatorial transverse section showing two lobes of the locule separated by primary septum, lacuna evident below as white line. k: Transverse section near base

al. 2018). Rather, the locule is lined by a bipartite locular envelope that opens "like a pair of lips or clam-like valves" (Herrera et al. 2018). These valves are not obvious and in un-germinated fruits may be covered by the exocarp, perhaps explaining the "bulge" illustrated over one of the locules in Text-fig. 5j. The other locules of the same specimen are open to the surface. Due to the lack of anatomical preservation, our assignment of this fossil remains tentative. However, the number of locules, and the bipartite inner locule lining are strongly suggestive of *Pleiogynium*.

Tribe Spondioideae Такнт.

Genus et species indet.
Text-fig. 5g–i

M a t e r i a l . One fruit replaced by chalcedony, USNM PAL 772358.

D e s c r i p t i o n . Endocarp subglobose, but wider below the equator than above, rounded-elliptical in transverse view, height 9.5 mm, diameter 11.7 mm × 12.3 mm. The base slightly rounded to flat, lacking any suggestion of an attachment point or ridges. The apical surface eroded and revealing seven locules, all but one represented by an elliptical pit. One locule covered by an apparent valve, but eroded such that further characters are lacking.

D i s c u s s i o n . This is clearly another fruit conforming to the Spondioideae. We recognize two Spondioid fruit types, cf. *Pentoperculum* Manchester and cf. *Pleiogynium* in the Wagon Bed flora based on the current distinctions in the literature, and consider that USNM 772358 likely belongs to one of these. However, it is difficult to place with certainty due to its eroded condition. Another option would be to consider these all of the specimens as the product of one highly variable, parent plant, but with preservation limiting the appreciation of different characters (e.g., variable locule number, presence of a bipartite operculum versus a bipartite locule lining).

The Spondioideae include 20 genera and some 115 species of pantropical and subtropical trees, all with fleshy, animal dispersed, fruits. The systematics of the group has seen flux and is summarized by Mitchell et al. (2006). The Anacardiaceae are represented in the pollen flora of the Wagon Bed Formation (Leopold and MacGinitie 1972) by *Rhus* L.

Family Burseraceae Kunth.

Genus *Canarium* L.
Text-fig. 5n–q

M a t e r i a l . One specimen, chalcedony cast, USNM PAL 772361.

D e s c r i p t i o n . Fruit elliptic in lateral view (Text-fig. 5n, o), rounded-triangular in cross section (Text-fig. 5p), 27 mm long with a minimum equatorial diameter of 15 mm and a maximum equatorial diameter of 17.6 mm, the variation likely due to slight compression. Each corner of the triangular cross-section defined by a ridge which is poorly defined at the base but becomes strongly expressed apically, the ribs curving in on each other at the apex, but not touching, instead over-arching a small apical point (Text-fig. 5p). Each ridge with a central groove, the groove more defined towards the apex. The three ridges separate three elongate embayments on each of the three sides of the endocarp (Text-fig. 5p). Each embayment has grooves adjacent to the adjoining ribs and a central groove running up the middle of the face, the three grooves defining two low, longitudinal ridges running up each face. Base with an ill-defined point of attachment.

D i s c u s s i o n . The shape of the fossil, coupled with the three strong longitudinal ridges, suggests a valvate endocarp, such as found in the Cornaceae L. (some *Nyssa* L., *Davidia* Baill.) or Verbenaceae J.St.-Hill.(e.g., *Tectona grandis* L.f.). However, the strength of the three lateral ridges and their overarching structure at the apex is most consistent with endocarps of *Canarium* involving a central, woody and resistant receptacle (see illustrations in Han et al. 2018). Interpreted as *Canarium*, then within the embayments formed by the receptacle are three separate endocarps enveloped by a common mesocarp and a fleshy exocarp (Leenhouts 1956, 1959). The mesocarp forms a germination valve over each locule that is shed at maturity (Hill 1933). While internal morphological and anatomical details to confirm this morphological interpretation are lacking, the presence of "*Canarium* type" pollen from the Wagon Bed Formation (Leopold and MacGinitie 1972) supports this interpretation. Also from this formation, Fiero and Jones (1990) report a wood that they felt could be attributed to one of four families, including the Burseraceae.

Fossil fruits of *Canarium* are known from the Paleogene of Europe (Gregor and Goth 1979, Collinson et al. 2012), Egypt (Bown et al. 1982) and New Jersey, USA (Tiffney 1999), and from the late Oligocene to Miocene in Asia (Han et al. 2018). Although the foliage of *Canarium* is not particularly distinctive, the genus has been reported based on leaflet impressions from the middle Eocene of northern (MacGinitie 1941) and southern (Myers 1990) California; Hickey (1977) described *Canariophyllum* L.J.Hickey from the latest Paleocene – early Eocene of North Dakota. Endocarps reported as *Bursericarpum* E.Reid et M.Chandler from the London Clay (Reid and Chandler 1933, Chandler 1961) and the Clarno Formation of Oregon (Manchester 1994) represent the same family, but they are individual pyrenes rather than the trilocular syncarpous fruit that characterizes *Canarium*.

of nut showing four lobes of the locule separated by primary and secondary septa. l: **Virtually extracted locule cast in two lateral views and in apical and basal view. m–q: USNM PAL 772354. m: Half nutshell, lateral surface view. n: Lateral view, rotated 90° from (m). o: Apical view, with radiating grooves. m, n, o: Micro-CT scan surface renderings. p: Internal view of nut naturally cleaved, displaying the locule, depth map image. q: Enlarged view in same orientation of (p), palladium-coated, reflected light, showing pseudo-cellular radiating mineral fibers. r–w:** *Carya* **USNM PAL 772348. r–t: Micro-CT scan surface renderings. r: Lateral surface view of smooth nutshell. s: Lateral view of nutshell half, rotated 90° from (r). t: Apical view of nutshell half. u: Basal view, showing radiating grooves, reflected light, palladium coated. v: Internal view of nutshell displaying the locule, micro-CT surface rendering. w: Same view, micro-CT depth map image.**
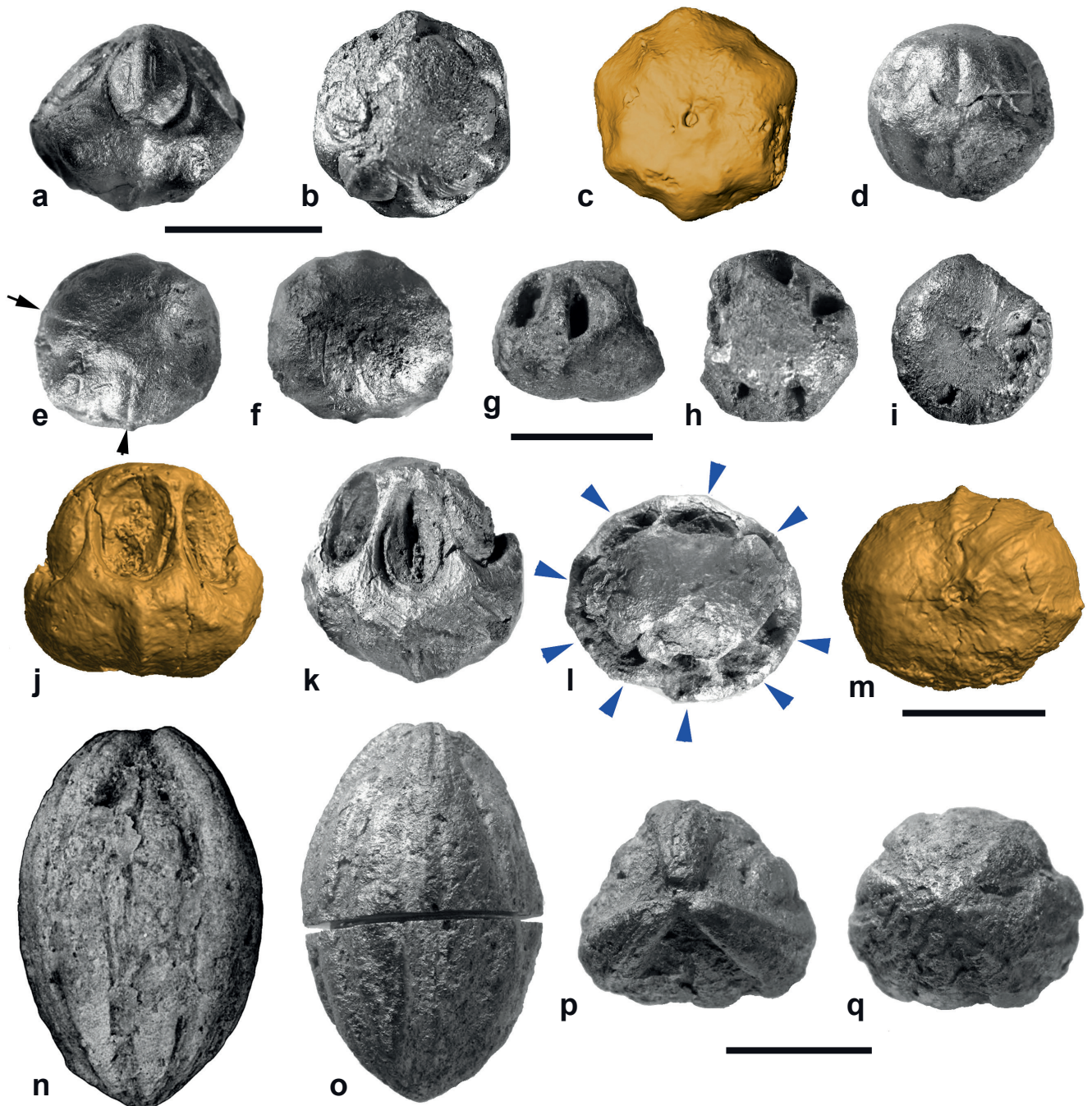
Text-fig. 5. Anacardiaceae (a–m), Burseraceae (n–q). Scale bars = 1 cm. a–f: *Pentoperculum* sp. a–c: USNM PAL 772360. a: Lateral view of endocarp, apex up; three germination valves visible, the central clearly displaying the bipartite nature of the valve, reflected light, palladium coated. b: Apical view displaying six locules, with two preserved germination valves at the lower left, reflected light, palladium coated. c: Basal view of the endocarp, the locules suggested by swellings; note point of attachment, micro-CT scan surface rendering. d–f: *Pentoperculum* sp. USNM PAL 772359, reflected light, palladium coated. d: Lateral view of a probable 6-loculed endocarp, apex up; a single intact germination valve in the center, displaying the central lineation that divides it in two. e: Apical view; two bi-partite germination valves are visible, indicated by arrows to the middle cleavage line of two of the valves. f: Basal view, the locules suggested by the undulations in the margin. g–i: Indet. Spondioideae. USNM PAL 772358, reflected light, palladium coated. g: Lateral view of multi-locular endocarp, apex up. h: Apical view showing finely punctuate surface and peripheral locule cavities. i: Basal view. j–m: Cf. *Pleiogynium* USNM PAL 772357. j: Lateral view of the multi-locular endocarp, apex up; note intact germination valve on left and exposed locule facing the viewer, micro-CT scan surface rendering. k: Lateral view, rotated about 30° from (j), showing three exposed locules, reflected light, palladium coated; note bipartite locule lining at center. l: Apical view of the multilocular endocarp; the locule with intact germination valve at the upper right, reflected light, palladium coated. Arrows to each locule. m: Basal view showing central point of attachment and prominent radiating ridges aligned with the locules, micro-CT scan surface rendering. n–q: *Canarium*, USNM PAL 772361. Scale bar = 1 cm. n: Lateral view of endocarp directly facing one germination valve flanked by two strong ridges; apex up; specimen coated in sodium nitrate and photographed by R. A. Scott. o: Lateral view facing one of the three pronounced ridges, flanked to the left and right by two germination valves; apex up. p: Apical view displaying the three strong ridges, arching over the apex and flanking three deep embayments, covered with germination valves. q: Basal view, the three ridges being less pronounced. o–q: Reflected light, palladium coated.

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The genus consists of 75 (Leenhouts 1959) to 108 species (Lam 1932) of the Old World tropics. According to Leenhouts (1959), three species are native to Africa, Madagascar and the Mauritius, two to Australia, and the remainder occur from India east through Melanesia. These include canopy trees, shrubs and "pseudolianas" (Leenhouts 1959) which generally inhabit low elevation primary and secondary rainforests in monsoonal climates.

Family Cornaceae L.

Genus *Alangium* Lam.
Text-fig. 6a–e

Material. One chalcedony cast, DMNH EPI.47806.

Description. Bilocular endocarp represented by two locule casts arranged in the form of a sandwich (Text-fig. 6c–e) with the intervening septum also silicified. Endocarp wall missing. Locules elliptical in face view (Text-fig. 6a, b), 13.8–16.3 mm long, 11.5–12.9 mm wide, each 3–4 mm thick, one slightly larger than the other; fruit 9.3 mm thick perpendicular to the septum. Septum ca. 1.5 mm thick, with about 16 regularly spaced peripheral circular depressions corresponding to the central vasculature (Text-fig. 6c–e).

Discussion. This distinctive cast was readily identified through comparison with similarly preserved specimens from the Clarno Formation of Oregon (Manchester 1994). The Clarno specimens exhibit a range of preservation modes from permineralized examples with sufficient anatomical detail to verify the generic determination, to chalcedony locule cast "sandwiches" like the one figured here. The Wagon Bed specimen conforms to endocarps of section *Marlea* (Roxb.) Baill., which is also known from other Eocene localities including the Clarno Formation (Manchester 1994), the London Clay (Chandler 1961) and Messel (Collinson et al. 2012) and from the Miocene Brandon Lignite (Eyde et al. 1969). This specimen is distinctive in its large size in comparison to other Eocene species (length of 16 mm in this species vs. 10 mm in Clarno, 11 in London Clay, 6 mm in Messel). The modern genus includes about 20 species of small trees, shrubs and lianes of the Old World tropics, dominantly of southeast Asia (Mabberley 2008). In sect. *Marlea*, *A. scandens* Bloemb. is noted as a climber (De Wilde and Duyfjes 2016).

Genus *Mastixia* Blume.
Text-figs 6f–r, 7a–e

Material. Four chalcedony casts. USNM PAL 772364, 772362, 772363, 772365.

Description. Endocarp ellipsoidal, longitudinally ribbed, unilocular (Text-figs 6f–k, 7a–c), with a u-shaped locule (Text-fig. 6r). Endocarp elliptic in lateral view, almost circular in cross-section, averaging 23.5 mm in length (range 20.7 mm to 27.2 mm) and 13.2 mm in diameter (range 11.4 mm to 16.1 mm) with a clear dorsal infold in some specimens (Text-fig. 6f, j, k, l, o, q). The best-preserved specimen (Text-fig. 6f–k) possesses low, discontinuous, rugose, longitudinal ridges about 1 mm in width, approximately 10 present at one end, 14 at the other; the eroded specimens possess

suggestions of similar ridges, although poorly preserved at one end. The ends of the intact specimen are marked by small protrusions, one with a small, cap-like structure against which the longitudinal ridges end (Text-fig. 6j) and the other formed by the coalescence of the longitudinal ridges (Text-fig. 6k). One eroded specimen has only one end preserved, this with a protrusion formed by the coalescence of the ridges while a second exhibits an apical cap against which the ridges abut in a manner similar to the intact specimen.

Discussion. The shape, rugose longitudinal ridges and the single prominent longitudinal groove are all consistent with the endocarps of some species of *Mastixia*, the groove being interpreted as the infold of the dorsal germination valve. Unfortunately, the preservation of these fossils as casts, lacking any permineralized tissues, precludes further validation. The fossils can be distinguished from *Mastixicarpum* M.Chandler, as they do not exhibit any sign of the persistent epicarp distinctive of that genus. Rather, it appears the epicarp was fleshy and thus lost as in extant *Mastixia*, exposing the endocarp. One of the specimens exhibits a semi-circular pit excavated on one side strongly suggestive of predation (Text-fig. 6m, n), perhaps by a rodent-like animal. A lesser gouge is visible on the surface of another specimen (Text-fig. 6h).

The occurrence of *Mastixia* in the Wagon Bed flora is not startling, as fruits conforming to this genus are known from the latest Paleocene to earliest Eocene Sand Draw flora and late early to early middle Eocene Sepulcher floras of Wyoming (Tiffney and Haggard 1996), as well as from the middle Eocene Clarno flora of Oregon (Manchester 1994) and late Eocene Auriferous Gravels of California (Tiffney and Haggard 1996). The genus is widespread in the European Tertiary (Mai 1993). Cornaceae was not observed in the pollen flora of the Wagon Bed Formation (Leopold and MacGinitie 1972), but wood with anatomy consistent with Nyssaceae (subsumed by some authorities along with Mastixiaceae into Cornaceae) and/or Styracaceae DC. et Spreng. is reported (J. H. Jones, pers. comm.). In the current day, *Mastixia* is represented by ca. 20 species of trees and shrubs in Indomalaysia and the Philippines through India (Matthew 1976), although more recent works have suggested a greater diversity (Liu and Peng 2009).

Genus cf. *Nyssa* L.
Text-fig. 7f–j

Material. One chalcedony cast, DMNH EPI.47808.

Description. Endocarp elongate-ellipsoidal (Text-fig. 7f–h), distinctly pointed at one (? apical) end, approaching three-angled in cross-section (Text-fig. 7j), partially damaged on one side. Length 28.3 mm, 10.5 mm in widest cross section, by 8.3 mm in narrowest. Surface traversed by 10 longitudinal ribs which are about ca. 2.0 mm broad at equator. No clear indication of a dorsal infold, locule not preserved. The upper 2/3 of one of the three faces (Text-fig. 7g, i) apparently removed before deposition, interpreted to indicate detachment of germination valve.

Discussion. This endocarp is similar to those of *Mastixia* (described above) but differs in its more elongate shape, trigonal, attenuated apex, lower number of ribs that are

Text-fig. 6. Cornaceae. *Alangium* (a–e), *Mastixia* (f–r). a–e: *Alangium*, DMNH EPI.47806. Scale bar = 1 cm. b, e: Reflected light, palladium coated. a, c, d: Micro-CT scan surface rendering. a: Locule cast, face view of slightly larger locule. b: Face view of slightly smaller locule. c: Lateral view of the endocarp, the slightly enlarged left carpel separated from the smaller carpel by a longitudinal septal groove; the faint pitting in the groove suggestive of the septal vasculature. d, e: Views of either end of the endocarp, illustrating the size difference between the two carpels and the pitting in the septal groove suggestive of the septal vasculature. f–k: *Mastixia* USNM PAL 772362. Scale bar = 1 cm. f, g, j, k: reflected light, palladium coated; h, i: micro-CT scan surface rendering. f: Lateral view of endocarp, inferred dorsal germination valve groove facing the viewer. Note irregular, rugose, longitudinal ridges. g: Lateral view of endocarp, inferred germination valve with median longitudinal groove to left. h: Lateral view of endocarp reoriented with the same longitudinal groove to the right. i: Lateral view, rotated to ventral surface. j: View of one end of the endocarp, germination valve groove up. k: Opposite end view, with prominent radial ridges and intervening grooves, germination valve groove up. l–r: *Mastixia* USNM PAL 772363. Scale bar = 1 cm. l: View of one face of endocarp, displaying a groove that may represent the surficial expression of the dorsal infold of a *Mastixia*-like germination valve. Surface badly eroded, reflected light, palladium coated. m: Opposite face of endocarp displaying extensive erosion and a central hole interpreted as feeding damage. n: Lateral view; m, n micro-CT scan surface renderings. o: A view of one end, displaying the prominent groove, reflected light, palladium coated. p: Opposite end to (o). q: View as in (o); p, q micro-CT scan surface renderings. r: Virtual transverse section showing curved locule (arrows).

broader, and apparent lack of an infold. The pre-depositional damage, here interpreted as the detachment of a partial apical valve, if correctly interpreted, is a feature distinctive of Nyssaceae, whereas germination valves of Mastixiaceae extend the full length of the endocarp. As with many of the other Wagon Bed specimens, it is a cast, lacking details of the internal structure. For this reason our identification as *Nyssa* remains tentative. Morphologically similar fruits, with internal morphology and anatomy preserved, confirm the presence of *Nyssa* in other Eocene floras in Europe (Reid and Chandler 1933) and North America (Manchester 1994). The specimen shows transverse abrasions (Text-fig. 7g) that may represent the gnaw marks of a mammalian seed-predator. *Nyssa* is represented by eight species of trees in the current day, distributed in North America (4 species), Central America (1), China (2) and Indomalaysia (1) (Zhou et al. 2020); the morphology of their fruits is central to their identification (Eyde 1963).

Family Icacinaceae MIERS

Genus *Iodes* BLUME
Text-fig. 7k–o

Material. One chalcedony cast, DMNH EPI.47807.

Description. Endocarp broadly oval/ovate in face view, strongly flattened perpendicular to the face view, creating a lenticular cross-section, 18.8 mm long, 15.0 mm wide in face view and 7.8 mm thick (Text-fig. 7k–o). The apex mildly pointed, the base rounded. A keel surrounds the endocarp, clearly grooved on one side in the position of the primary vascular bundle, extending from the base to the apex (Text-fig. 7m). The surface of the endocarp traversed by an anastomosing pattern of ridges creating a reticulum that separate a series of depressions or pits; while some ridges traverse the length of the endocarp, others are less strong and end within the depressions.

Discussion. The ovoid outline in face view and flattened cross section, coupled with the surficial reticulation and primary vascular bundle running along one of the lateral keels, all conform to *Iodes*. As it is a cast without internal preservation, the precise position of the primary bundle, whether within the endocarp wall, or immediately outside, is not clear. Still, the external morphology strongly conforms to that of *Iodes*. Further, fossils of *Iodes* are common in the Eocene of North America, and Eurasia (Stull et al. 2016, Del Rio et al. 2019). The modern genus comprises circa 28 species of lianas found in Africa, Madagascar and subtropical Asia (Mabberly 2008). *Iodes* joins *Chandlera* in representing vines in the Wagon Bed flora. The Icacinaceae is also represented in the Wagon Bed flora by pollen (Leopold and MacGinitie 1972).

Genus *Carpolithes* BRONGN.
Carpolithes sp. 1
Text-fig. 8a–e

Material. One specimen, chalcedony cast, USNM PAL 772366.

Description. Ovoid to obovoid in lateral view, inflated, three sided in cross section (Text-fig. 8a–c). 13.4 mm long, 8.2 by 8.4 mm in cross section. Two of the three angles defined by strong longitudinal ridges, the third angle eroded, without a pronounced ridge (Text-fig. 8d). The most pronounced ridge bounded by two faint lineations that meet near the more rounded end. The faces between the ridges (where not eroded) with fainter longitudinal striations. The rounded end with a small, circular raised point, possibly of attachment. The opposite end more pointed, but with the tip eroded. The structure is almost split in half at the more pointed end.

Discussion. The presence of a scar on the rounded end leads us to postulate that this is the base, although that might be in error. The size and three angled aspect of the fossil, coupled with the faint lineations adjacent to the most well-developed ridge, led to the initial hypotheses that this might be a three-angled endocarp with three valves, perhaps like *Nyssa*. However, these potential valves are more elongate than those of *Nyssa*, which has valves limited to the apical half of the endocarp. If it were *Nyssa*, this would also suggest that the scar on the rounded end was in fact associated with the stigma, and that the pointed and eroded end was the base. However, in the absence of further detail, we choose to treat this as *Carpolithes*.

Carpolithes sp. 2
Text-fig. 8f–j

Material. One specimen, chalcedony cast, USNM PAL 772367.

Description. Disseminule narrowly ovate to ovate in lateral view, nearly circular in cross section, 9.6 mm in length, 5.6 by 5.7 mm in cross section. The broad basal end has a central point of attachment, lateral to which on one side is a distinct structure consisting of two parallel smooth lineations flanking a wider, raised, central zone of elongate cells (Text-fig. 8f). This extends approximately 40% of the length of the structure before being obliterated by erosion of the surface. A very faint single line occurs on the opposing margin of the structure, extending about 50% of the length of the structure before similarly being eradicated by erosion of the surface of the object.

Discussion. The basal scar and particularly the well-developed lineation on one side suggest that this could be interpreted as a seed with a lateral vascular strand or raphe. However, the apical end of the seed is badly eroded so that the full path of the raphe-like structure cannot be traced. There is a similarity in form and size to the seeds of *Nuphar* SM. (Nymphaeaceae SALISB.), but details of the cellular structure and operculum are not available to confirm its identity.

Carpolithes sp. 3
Text-fig. 8k–o

Material. One specimen, chalcedony cast, USNM PAL 772368.

Description. Seed, broadly ovate in lateral view, elliptic in cross section, 6.1 mm high, 6 mm in diameter perpendicular plane of symmetry and 7.5 mm parallel to it. Apex with a prominent extension, 2.7 mm in diameter and 1.5 mm in height, flared at it distal tip (Text-fig. 8k–m),
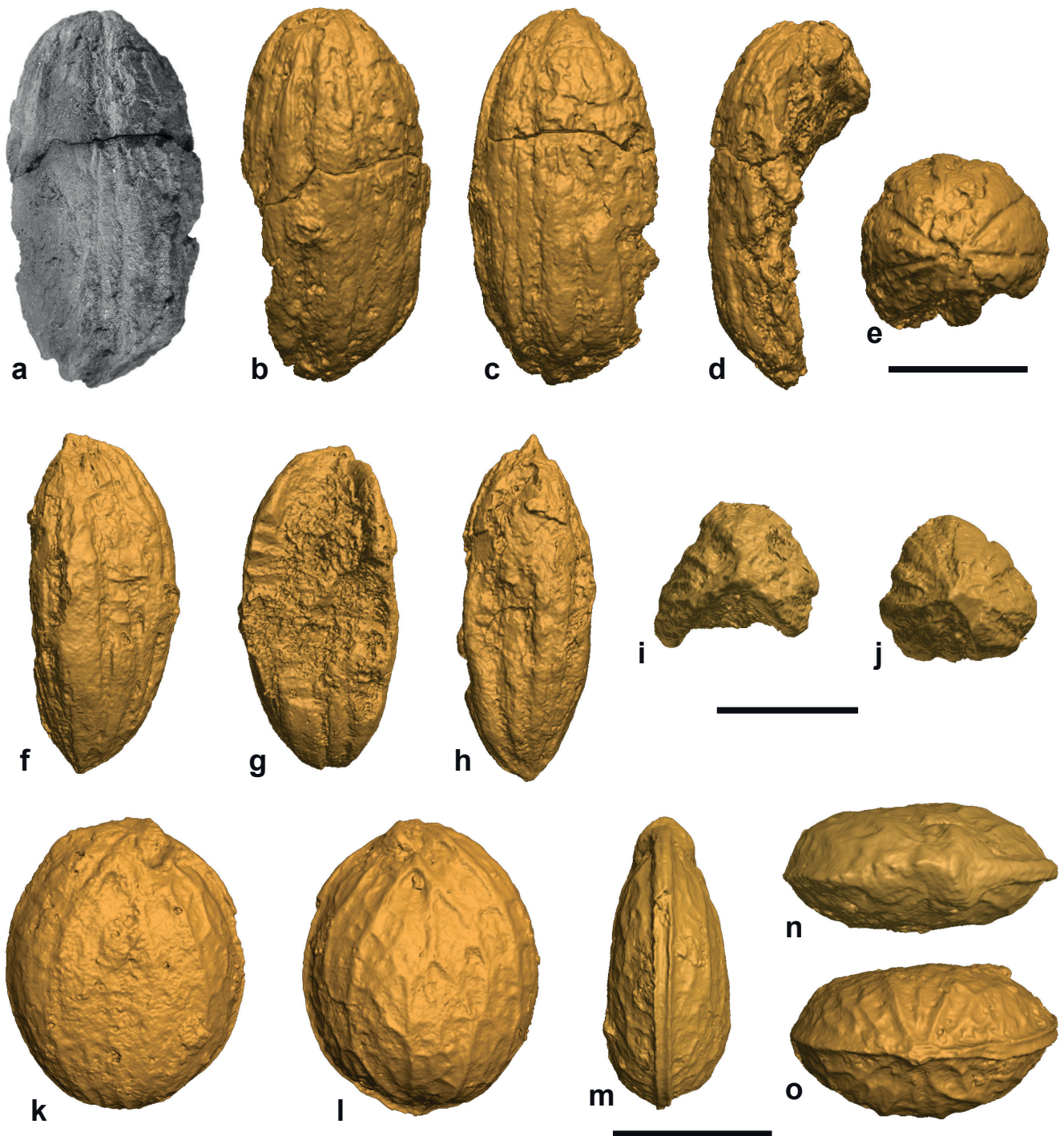
Text-fig. 7. Cornacaeae (a–j), Icacinaceae (k–o). a–e: *Mastixia.* USNM PAL 772364. Scale bar = 1 cm. a: Lateral view of eroded endocarp – the opposite side being missing and the endocarp broken near its mid point, reflected light, palladium coated. b–e: Micro-CT scan surface renderings. b: Rotated 90° from the view in (a). c: Rotated 90° from the view in (b). d: Rotated 90° from (c), exhibiting the damaged "back" face of the endocarp. e: Axillary view of the endocarp; the opposite end missing as apparent in (d). f–j: Cf. *Nyssa.* DMNH EPI.47808. Scale bar = 1 cm. Micro-CT scan surface renderings. f: Intact face of the endocarp; note ridges and "apical" point. g: Eroded (?gnawed; note horizontal grooving) opposite face of the endocarp. h: Lateral view of the endocarp, eroded/gnawed face to left. i: Apical view, eroded/gnawn portion below. j: Basal view of endocarp. k–o: *Iodes* DMNH-EPI.47807. Micro-CT scan surface renderings. Scale bar = 1 cm. k: Face view of endocarp. l: Opposite face of endocarp. m: Lateral view demonstrating the compressed nature of the endocarp, note thickened suture marking the probable track of the primary bundle. n: Apical view, primary bundle trace to right. o: Basal view, primary bundle trace to right.

with a central cylindrical aperture (Text-fig. 8n). A distinct groove runs along one side from the apical extension, down the side away from the offset, fading into the surface just before reaching the base (Text-fig. 8k, n). The surface with a very faint reticulate pattern (Text-fig. 8l, lower left).

D i s c u s s i o n . We interpret this as either an anatropous seed or locule cast, possibly with an intact aril and with a prominent groove, possibly a raphe, running medially from the apex to a basal chalaza. The fact that a strong groove is not present on both sides of the seed, and that it fades
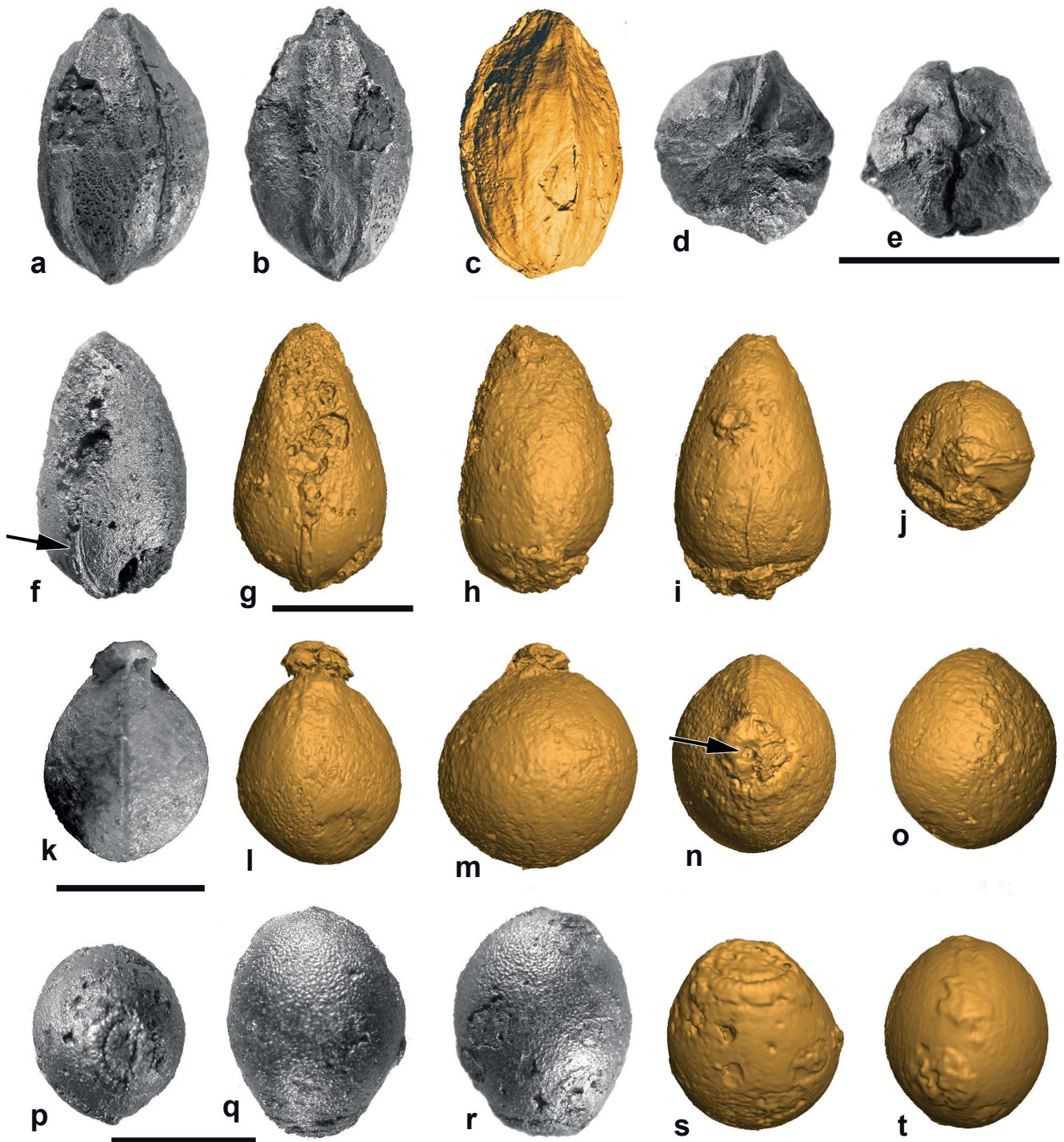
Text-fig. 8. *Carpolithes* (a–t). a–e: *Carpolithes* sp. 1. USNM PAL 772366. Scale bar = 1 cm. a: Lateral view of endocarp, note two longitudinal ridges. b: Lateral view of endocarp rotated 90° from (a), note single lateral ridge in center, a, b reflected light, palladium coated. c: Lateral view, Micro-CT scan surface rendering. d: View of rounded end of the endocarp, reflected light, palladium coated. e: View of the opposite (pointed) end of the endocarp, note split; reflected light, palladium coated. f–j: *Carpolithes* sp. 2. USNM PAL 772367. Scale bar = 5 mm. f: Lateral view, base down; note raphe-like structure (arrow), reflected light, palladium coated. g: Lateral view, the raphe-like structure extending vertically from the base. h: Lateral view, rotated 90° from (g). i: Lateral view, the opposite face to that in (h). j: Basal view, raphe-like structure running from the center to the right of the image. g–j: CT scan surface renderings. k–o: *Carpolithes* sp. 3 USNM PAL 772368. Scale bar = 5 mm. k: Ventral view of the specimen, note flared apical extension, reflected light, uncoated. l: Dorsal view illustrating the flared apical extension, rotated 180° from (k). m: Lateral view rotated 90° from that in (l). n: Apical view, the apical extension with central pore (arrow) and a clear lineation running down the side to the top of the image. o: Basal view. l–o: Micro-CT scan surface renderings. p–t: *Carpolithes* sp. 4. USNM PAL 772369. Scale bar = 3 mm. p: Basal view illustrating the concentric rings of radiating possible cells surrounding a central depression. q: Lateral view, base down, note possible cellular pattern. r: Lateral view, rotated 180° from (q), base down; p–r: reflected light, palladium coated. s, t: Basal and lateral views, micro-CT scan surface renderings.

towards the base, suggests that it is a raphe and not a plane of dehiscence. The prominence of the apical extension could reflect a piece of adherent seed coat, but its symmetry and the central apical canal (micropylar?) suggests a caruncle, like that of Euphorbiaceae Juss.

The rounded base, carunculate apex, prominent raphe, and surface cellular pattern are consistent with Euphorbiaceae. It may be appropriate to place this in the fossil genus *Euphorbiospermum* E.Reid et M.Chandler, which was established to accommodate seeds clearly referable to the Euphorbiaceae but for which extant generic affinities are not known (Reid and Chandler 1933). Although the several London Clay species that Reid and Chandler placed in the genus do not preserve the arils, they typically possess a hilar truncation consisting of a pair of oblique ventral facets forming a broad angle of 100 to 130 degrees that likely indicates the position of the caruncle. Although the softer lipid-rich tissue of the caruncle might not be expected to preserve, it has been shown to preserve in casts of seeds within euphorbiaceous fruit from the early Oligocene of Peru (Hamersma et al. 2022). Alternatively, the apical extension could suggest that this was a seed that was surrounded by a fleshy layer in life that was mostly not preserved except for the remaining apical fragment.

Carpolithes sp. 4
Text-fig. 8p–t

M a t e r i a l . One specimen, chalcedony cast, USNM PAL 772369.

D e s c r i p t i o n . Ovate-elliptic in lateral view, elliptic in cross-section, 5.5 mm high, 4.1 by 3.6 mm in cross section. Attachment end with a collar-like opening (Text-fig. 8p, s), 1 mm diameter, with a slight central depression surrounded by a two raised, concentric rings, each with a rounded margin bearing a faint hint of radially-oriented cells (Text-fig. 8p). The surface of the fossil marked by a faint papillate pattern suggestive of cells (Text-fig. 8q, r). Distal end rounded, without any distinctive markings.

D i s c u s s i o n . The short and long cross-sectional axes impart a bilateral symmetry to the structure, but there is no sign of a ridge or groove that would suggest a plane of dehiscence or raphe. The basal (?) scar is suggestive of a point of attachment. These features, coupled with a consistent surficial pattern indicative of cells, clearly indicate that this is a fruit or seed, but do not permit further attribution.

Carpolithes sp. 5
Text-fig. 9a–d

M a t e r i a l . One specimen, chalcedony cast, USNM PAL 772370.

D e s c r i p t i o n . Seed broadly elliptic in face view, 7.8 mm long, slightly dorsiventrally flattened, 5.8 mm by 4.9 mm, oval in cross-section. Seed with a circular, raised point of attachment with a central depression. Lateral to this on one side is a raised ridge that parallels one margin of the wider axis, disappearing into the seed margin about halfway along its length (Text-fig. 9a, d). Surface peeling off in a manner suggestive of cell layers (Text-fig. 9c), but more likely erosional. No internal structure apparent.

D i s c u s s i o n . *Carpolithes* species 5 is interpreted as an anatropous seed with an adjacent apical hilum and micropyle, and a subtending lateral raphe, melding into the seed about halfway down the margin. In these characters, they bear a resemblance to the seeds of Nymphaeaceae L. However, the separation of the hilum and micropyle is not distinct as in many Nymphaeaceae, and no details of the cellular structure of the seed coat are apparent, both critical in making a more certain assignment.

Carpolithes sp. 6
Text-fig. 9e–h

M a t e r i a l . One specimen, chalcedony cast, USNM PAL 772371.

D e s c r i p t i o n . Disseminule broadly elliptic in face view, narrowly elliptic in cross-section, 8.3 mm long, dorsiventrally flattened, 7.5 mm by 5.0 mm. Possessing a circular, raised point of attachment with a central depression (Text-fig. 9e). Lateral to this on one side is a raised ridge that parallels one margin of the wider axis, disappearing into the margin about half way along its length.

D i s c u s s i o n . *Carpolithes* species 6 bears resemblance to the endocarp of *Prunus*, with a prominent longitudinal keel in the plane of bisymmetry. The keel on one lateral margin is sharper than on the other. Details of the vascular supply that could help to confirm or disprove this possible affinity are not preserved.

Carpolithes sp. 7
Text-fig. 9i–m

M a t e r i a l . One specimen, chalcedony cast, USNM PAL 772372.

D e s c r i p t i o n . A broken half sphere, 10.9 mm in height and 9.7 mm wide, the thickness (through the broken portion), 5.4 mm. The surface is rough (Text-fig. 9i), although it is unclear if this is due to adherent minerals or represents the original condition. One end has a slight constriction suggesting a point of attachment (Text-fig. 9i, j); the opposite end is smoothly rounded. In cross section, a palisade layer of a single layer of elongate sclereids is preserved, ranging from 0.5 to 0.85 mm in thickness (Text-fig. 9l, m). In places this has peeled off the exterior of the fossil. No further internal structure is present.

D i s c u s s i o n . The palisade layer of cells (Text-fig. 9l, m) indicates the botanical nature of this structure. The spherical shape, palisade layer of elongate cells and possible small point of attachment are reminiscent of the drupes of some Lauraceae Juss., but the material is not sufficiently well preserved to verify this assignment.

Carpolithes sp. 8
Text-fig. 9n–p

M a t e r i a l . One specimen, chalcedony cast, USNM PAL 772373.
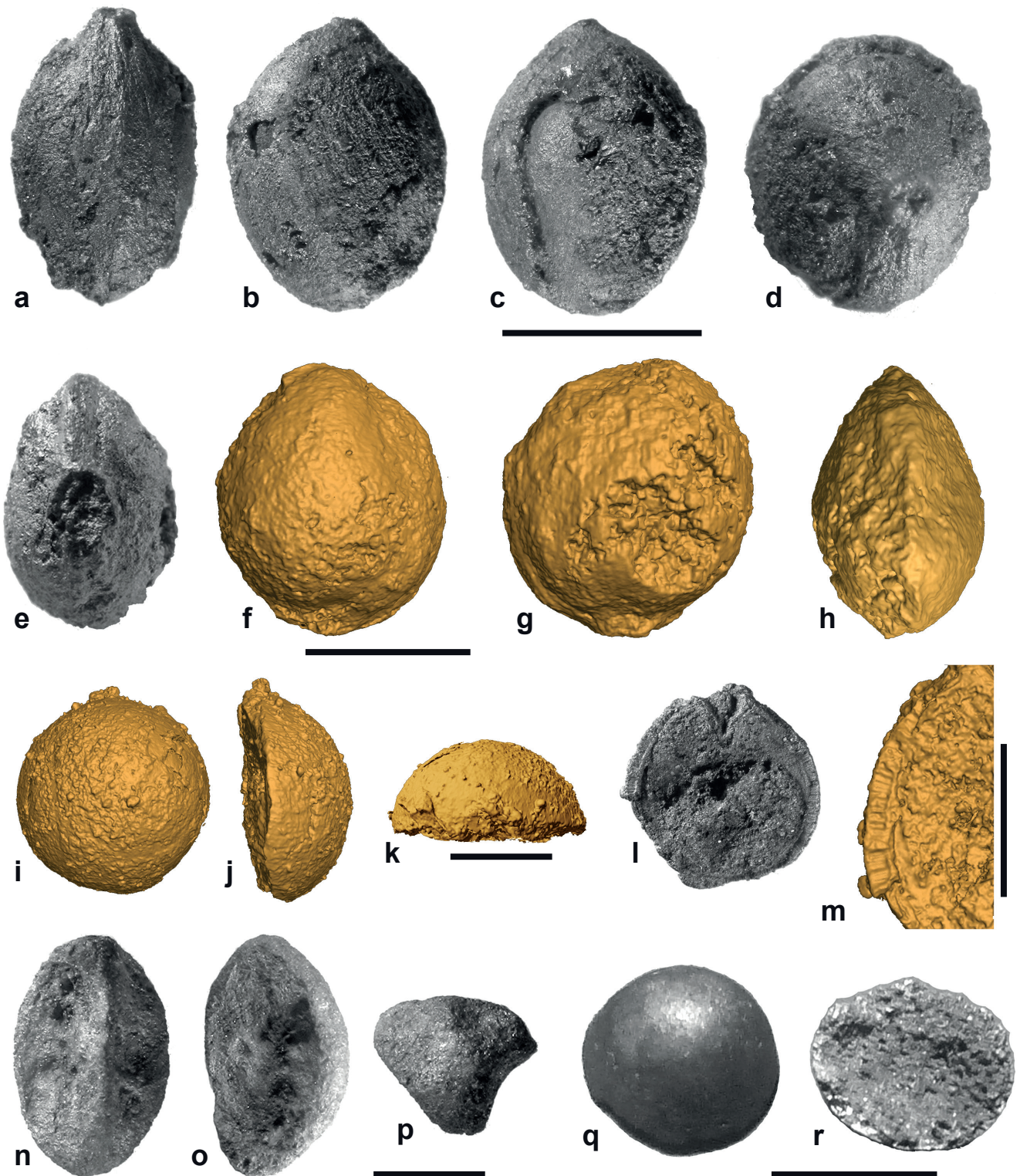
Text-fig. 9. *Carpolithes* (a–r). a–d: *Carpolithes* sp. 5. USNM PAL 772370. Scale bar = 5 mm, reflected light, palladium coated. a: Lateral view of seed, apex up, possible raphe descending from apex toward viewer. b: Lateral view of seed, apex up, possible raphe on right. c: Lateral view, opposite side, apex up, possible raphe on left. d: Apical view, note central pit with raphe descending towards bottom margin. e–h: *Carpolithes* sp. 6. USNM PAL 772371. Scale bar = 5 mm. e: Basal view illustrating depression and keel in plane of bisymmetry, reflected light, palladium coated. f–h: Micro-CT scan surface rendering. f: Lateral view showing relatively smooth rounded surface. g: Specimen rotated 180° from (f), surface partially eroded. h: Longitudinal view, showing median keel. i–m: *Carpolithes* sp. 7 USNM PAL 772372. Scale bar = 5 mm. i: View of intact face of globose fruit, possible apical constriction at top. j: Lateral view, intact surface to right, possible apical constriction at top, both micro-CT scan surface renderings. k: Apical view. l: Face view illustrating the mineral filling and the fine, radiating structure of the fruit wall on the left and right margins, both reflected light, palladium coated. m: Closeup of the cellular layer on the left of (l), micro-CT scan surface rendering. n–p: *Carpolithes* sp. 8. USNM PAL 772373. Scale bar = 3 mm, reflected light, palladium coated. n: Lateral view of pyrene-like structure, one ridge running vertically in the center of view, the other two forming the left and right margins. o: Lateral view of pyrene-like structure, ridge in (n) on the left. p: End-on view illustrating one convex, one concave, and one relatively flat to very slightly concave face. q, r: *Carpolithes* sp. 9 USNM PAL 772374. Scale bar = 5 mm, reflected light, palladium coated. q: Exterior of the smooth broken half-sphere. r: Interior of the broken half-sphere.

Description. Elliptic in lateral view, three-angled in cross section, 6 mm in length, 4.9 mm at its widest cross-sectional view, 3.6 mm at its narrowest. The cross-section presents one slightly convex margin, the second flat and the third mildly concave (Text-fig. 9p). No clear point of attachment.

Discussion. The three-angled cross section is suggestive of a pyrene, with a rounded dorsal face and two flattened to concave lateral faces, such as might be found in some Rosaceae Juss., e.g., *Crataegus* L.. However, no further data can be observed to suggest that this is indeed biological in origin.

Carpolithes sp. 9
Text-fig. 9q, r

Material. One specimen, chalcedony cast, USNM PAL 772374.

Description. A half spherical to broadly elliptical structure in lateral view and cross section, 5.3 by 4.9 mm in cross section, the height on the broken axis 3.15 mm, suggesting an overall height of about 6 mm. The surface of the structure very smooth, possibly with a faint cellular pattern. No internal structure or evidence of a cellular wall in cross-section.

Discussion. The smooth, spherical shape of this structure, coupled with the possible faint surficial pattern of cells suggests it is possibly a seed, but we can offer no further attribution.
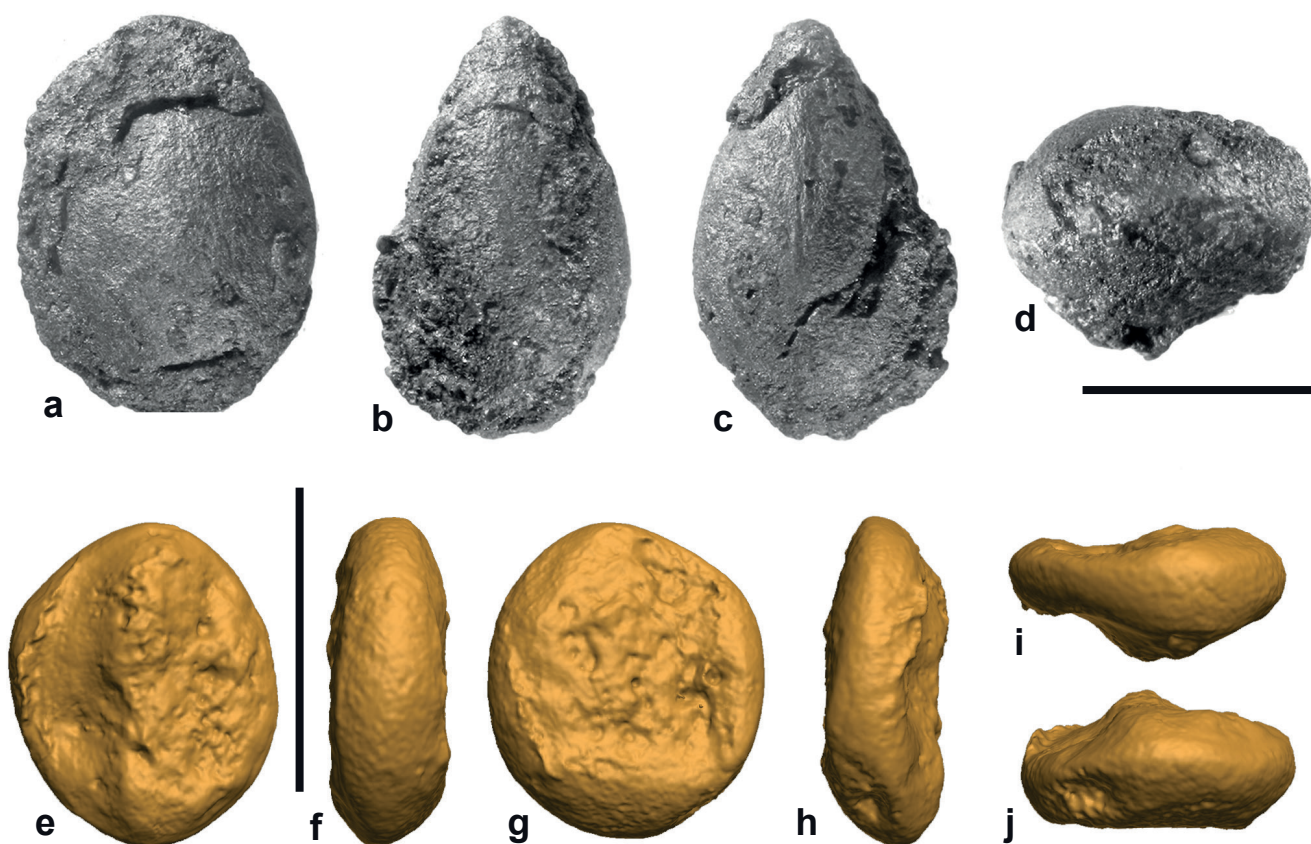
Carpolithes sp. 10
Text-fig. 10a–d

Material. One specimen, chalcedony cast, USNM PAL 772375.

Description. Elliptic in lateral view, narrowly elliptic in cross section, tapering from the inferred base to the apex, 9.8 mm in length, 7.2 mm by 5.8 mm in widest cross section. Surface largely obscured by adherent sediment forming a rough texture, but missing on one side, revealing a smooth, finely textured surface with a thin longitudinal groove flanked by two low ridges (Text-fig. 10c). Base and apex obscured.

Discussion. The adherent sediment likely reflects the mold that enclosed the cast of the original structure which is only partially exposed. The thin groove is suggestive of a point of dehiscence, although it might also be a raphe; the absence of data from both sides of the specimen makes this impossible to decide.

Carpolithes sp. 11
Text fig. 10e–j

Material. Six specimens, chalcedony, including USNM PAL 772376, 772377.

Text-fig. 10. *Carpolithes* (a–j). a–d: *Carpolithes* sp. 10. USNM PAL 772375. Scale bar = 5 mm, reflected light, palladium coated. a: Lateral view of one face of structure; note adherent mineral material. Longitudinal groove is to right. b: Lateral view of one edge of the structure. c: Opposite view from (b), note groove in upper half of the specimen, facing viewer. d: Apical view. e–j: *Carpolithes* sp. 11. USNM PAL 772376. Scale bar = 5 mm, micro-CT scan surface views. e: Structure in face view showing central protuberance. f: Same, lateral view. g: Opposite face from (e). h: Opposite face from (f). i: View from one end. j: View from opposite end from (i).

Description. Items round in face view, a flattened ovoid in lateral view. One face generally broadly convex and flattened, the other often slightly concave to flat with a central or slightly lateral emergent ridge or protuberance. Surface generally smooth. 2.0 to 3.3 mm thick, ranging from 4.4 by 4.8 mm to 6.9 by 5.3 mm in diameter.

Discussion. The repetitive morphology of these structures was distinctive and suggestive of a biological origin, although there is no evidence of possible cellular structure or of distinctive features (e.g., lineations) that would indicate vasculature or dehiscence. While we illustrate one of these examples here as *Carpolithes*, we suspect they may be abiotic.

General discussion

The total flora of fruits, seeds, pollen and wood (Tab. 1) incudes clearly identified representatives of 22 families; an additional four families might be represented by fruits or seeds if the tentative attributions offered in the text are correct. Further diversity might be present among the woods, where family attribution is not as certain in some cases.

The modern geographic and climatic affinities of these taxa are variable. *Carya* occurs in temperate portions of North America, Central America and eastern Asia, with a subtropical outlier, *C. poilanei* (Zhang et al. 2022. *Celtis* is pantropical with a few temperate outliers in Eurasia and North America, and members of the tribe Spondioideae of the Anacardiaceae are pantropical. *Canarium* is a tropical to subtropical tree of predominantly Indomalaysian distribution with a few species in Africa; *Mastixia* and *Pandanus* have tropical and subtropical representatives ranging from Indomalaysia, east to Madagascar, and in the case of *Pandanus*, south to northern Australia. *Alangium* occurs in the Old World tropics, with temperate Old World outliers, and *Aphananthe* occurs in the Old World tropics and subtropics with one species in Mexico. *Nyssa* occurs in temperate to subtropical environments in northern and Central America and eastern Asia. However, these modern climatic affinities may be misleading in light of the equable climates inferred for the Eocene (Wing and Greenwood 1993, Greenwood and Wing 1995) that accommodated mixed floristic assemblages composed of modern temperate and tropical taxa (e.g., Chandler 1961, Manchester 1994, Fairon-Demaret and Smith 2002, Collinson et al. 2012).

Leopold and MacGinitie (1972: 171) allied the Wagon Bed pollen flora with the early middle Eocene Kisinger Lakes and Tipperary floras, suggesting that all existed under a warm and humid climate supporting "a modified evergreen, broadleaved, sclerophyllous forest" that gave way to dryer conditions in the middle part of the middle and into the late Eocene, as reflected by the Florissant floras (MacGinitie 1974, Boyle et al. 2008, Leopold et al. 2008). The evidence from the co-occurring fruits and seeds suggests a more moist vegetation, perhaps reflecting a gallery or river margin forest embedded in a drier environment.

Of the Wagon Bed fruits and seeds, only *Mastixia* and *Iodes* are currently known to be held in common with the late Paleocene Sand Draw carpoflora of Wyoming (Keefer 1961, Tiffney and Manchester, unpublished data) which is just 3 km distant from the Wagon Bed locality. While the Sand Draw flora is still under investigation, this low degree of similarity would be consonant with the pattern of change in North American Paleogene floras described by Pigg and DeVore (2010). Only *Mastixia* and *Celtis* of the Wagon Bed flora are among the "Key taxa" that Pigg and DeVore list for the late Paleocene and early Eocene, a time of transition towards warmer and more moisture-rich floras, reflected in a diversification of taxa. Whether some of these newer taxa arose in North America and then migrated to the Old World via the North Atlantic or Bering Bridges or vice versa is unclear, and indeed a complex pattern of separate originations and migrations seems most likely (Tiffney 1985a, b, Manchester 1999). The Wagon Bed plants suggest a strong floristic continuity from the Rocky Mountains to the west coast of North America in the middle Eocene. *Alangium*, *Aphananthe*, *Chandlera*, ?*Coryloides*, *Mastixia*, *Nyssa*, *Saxifragispermum* and Spondioideae are held in common with the middle Eocene Clarno flora of Oregon (Manchester 1994). Similar affinities are exhibited with the floras of the Princeton Chert (Stockey et al. 1997b), and the Appian Way (Rankin et al. 2008) of British Columbia, and the late Eocene Auriferous Gravels floras of California (Tiffney and Haggard 1996). This continuity disintegrated with drying and cooling climates in the later Eocene, restricting paleotropical elements to the west coast (Wolfe 1971, 1978, 1987).

Further afield, the Wagon Bed fruits and seeds share affinities with European Eocene fruit and seed floras. *Alangium*, *Carya* (from pollen), *Mastixia*, *Nyssa*, *Saxifragispermum* and the Spondioideae of the Anacardiaceae also occur in the early Eocene London Clay (Chandler 1961). The London Clay fossil, *Tricarpellites communis* Reid et Chandler has been suspected to be similar to *Canarium* (Collinson et al. 2012), and *Canarium* has also been recognized from the early Eocene of Virginia (Tiffney 1999). The middle Eocene Messel flora of Germany similarly shares *Alangium*, *Aphananthe*, *Canarium*, *Mastixia* and Spondioideae with the Wagon Bed flora (Collinson et al. 2012).

One notable distinction between the Wagon Bed flora and these other floras is the low diversity of vines in the Wagon Bed. Taxa representing vines are normally common, comprising up to one third of the species diversity of other early to middle Eocene floras, but are represented with confidence in the Wagon Bed fruit and seed flora only by *Chandlera* (Menispermaceae) and *Iodes* (Icacinaceae), although some taxa of *Canarium* are pseudo-lianes, and one species of *Alangium*, sect. *Marlea* is a climber (De Wilde and Duyfjes 2016). In particular, the absence of representatives of the Vitaceae Juss. is noteworthy, as they are often common in other Eocene floras (Chandler 1961, Manchester 1994, Fairon-Demaret and Smith 2002). This might be a function of the small sample size of the Wagon Bed flora, and/or taphonomic sorting and collector bias favoring larger disseminules, but in the similarly small sample from the Virginian Eocene (Tiffney 1999) Vitaceae are present.

There are currently no reports of mammals from the strata in the immediate vicinity of the fossil flora. However, mammalian fossils are common in the Wagon Bed

Formation on the northeast side of the Wind River Basin near Badwater Creek, where fossils ranging from Bridgerian (middle Eocene) through Duchesnean (late Eocene) have been reported (Krishtalka et al. 1987). These include diverse late Eocene assemblages of insectivores and dermopterans (Krishtalka and Setoguchi 1977), artiodactyls (Black 1978) and carnivores (Dawson 1980), among others. Black (1978) notes in particular that the record of the artiodactyls in the Wagon Bed Formation is dominated throughout the Bridgerian-Duchesnean sequence by selenodont herbivores (those bearing teeth with crescentic ridges adapted to chewing resistant vegetation and often associated with ruminants). However, Artiodactyls with bunodont dentition (teeth adapted to chewing less resistant vegetation or perhaps crushing fruits and or seeds) are also present, but are almost entirely restricted to the earlier faunas. Black (1978) interprets this as evidence for a transition from a moist, more forested vegetation in the early middle Eocene towards a savanna woodland or savanna vegetation in the later middle Eocene and late Eocene in the Rocky Mountains. This is in agreement with the pattern noted by Leopold and MacGinitie (1972) and Wilf (2000) from plant evidence. Although of limited diversity, the Wagon Bed carpoflora is dominated by forest taxa that are generally not associated with savannas, although *Celtis* may be found in such circumstances. However, the coexistence of selenodont and bunodont mammals in the early middle Eocene portions of the Wagon Bed Formation suggests drier communities were present, but not preserved in the Wagon Bed flora.

The relatively large size of several of the Wagon Bed fruits (e.g., *Alangium*, *Canarium*, *Carya*, *Celtis*, *Chandlera*, ?*Coryloides*, *Iodes*, *Mastixia*, *Nyssa*, ?Pandanaceae, Spondioideae), also suggests the presence of a closed, shaded forest, rather than a more open environment favoring smaller seeds (Harper et al. 1970, Tiffney 1984). Only *Saxifragispermum* of the fruits and seeds within the flora suggests wind dispersal, although some taxa represented by pollen (e.g., *Acer* L., *Alnus* L.?, Bombacaceae Kunth, *Eucommia* Oliv., Malvaceae Juss., *Ulmus*/*Zelkova*; Leopold and MacGinitie 1972) might also have been wind dispersed. Given that pollen samples a larger area than do megafossils, these taxa may well represent a drier vegetation that was farther from the site of deposition.

Large seeds and fruits tend to be animal dispersed (Harper et al. 1970, Tiffney 1984). Several of the Wagon Bed fruits are inferred to have possessed fleshy exocarps (*Canarium*, *Celtis*, *Chandlera*, *Mastixia*, *Nyssa*, ?Pandanaceae, Spondioideae) and/or presented the reward of stored food reserves (*Carya*), suggesting their dispersal by coeval birds, rodents, or possibly primates. Indeed, one specimen of *Mastixia* (Text-fig. 6m) and one of *Nyssa* (Text-fig. 7g, i) exhibit what we could interpret as signs of mammalian, possibly rodent, predation. Indeed the damage shown in Text-fig. 6m is quite similar to the that interpreted as gnaw marks in fig. 5a, b of Huegele and Manchester (2019). While we are not aware of any rodents reported from the precise level of the Wagon Bed flora, it is noteworthy they are known from the underlying Fort Union Formation (Gazin 1971) and Wasatchian sediments (Gunnell et al. 2016, Strait et al. 2016), as well as the overlying Uintan portion of the Wagon Bed flora (Krishtalka 1978).

In sum, taking into consideration the collective evidence from vertebrates, fruits and seeds and pollen, it is possible that the Wagon Bed flora represented a moist, subtropical gallery forest adjacent to water in an otherwise already drying broader environment.

Acknowledgements

References

Allen, S. E., Stull, G. W., Manchester, S. R. (2015): Icacinaceae from the Eocene of western North America. – American Journal of Botany, 102: 725–744.
https://doi.org/10.3732/ajb.1400550

APG IV 2016 [Chase, M. W., Christenhusz, M. J. M., Fay, M. F., Byng, J. W., Judd, W. S., Soltis, D. E., Mabberley, D. J., Sennikov, A. N., Soltis, P. S., Stevens, P. F] (2016): An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. – Botanical Journal of the Linnean Society, 181(1):1–20.
https://doi.org/10.1111/boj.12385

Black, C. C. (1978): Paleontology and geology of the Badwater Creek area, central Wyoming. Part 14. The Artiodactyls. – Annals of the Carnegie Museum of Natural History, 47: 223–259.

Boles, J. R., Surdam, R. C. (1979): Diagenesis of volcanogenic sediments in a Tertiary saline lake, Wagon Bed Formation, Wyoming. – American Journal of Science, 279: 832–853.
https://doi.org/10.2475/ajs.279.7.832

Boucher, L. D., Manchester, S. R., Judd, W. S. (2003): An extinct genus of Salicaceae based on twigs with attached flowers, fruits, and foliage from the Eocene Green River Formation of Utah and Colorado, USA. – American Journal of Botany, 90: 1389–1399.
https://doi.org/10.3732/ajb.90.9.1389

Bown, T. M., Kraus, M. J., Wing, S. L., Fleagle, J. G., Tiffney, B. H., Simons, E. L., Vondra, C. F. (1982): The Fayum primate forest revisited. – Journal of Human Evolution, 11: 603–632.
https://doi.org/10.1016/S0047-2484(82)80008-0

Boyle, B., Enquist, B. J., Meyer, H. W., Salas, S. (2008): Higher taxa as paleoecological and paleoclimatic indicators: A search for the modern analog of the Florissant fossil flora. – In: Meyer, H. W., Smith, D. M. (eds), Paleontology of the Upper Eocene Florissant Formation, Colorado. Geological Society of America Special Paper, 435: 33–51. https://doi.org/10.1130/2008.2435(03)

Brown, R. W. (1959): Some paleobotanical problematica. – Journal of Paleontology, 33: 120–124.

Brown, R. W. (1962): The Paleocene floras of the Rocky Mountains and Great Plains. – U.S. Geological Survey Professional Paper, 375: 1–119. https://doi.org/10.3133/pp375

Buerki, S., Callmander, M. W., Devey, D. S., Chappell, L., Gallaher, T., Munzinger, J., Haevermans, T., Forest, F. (2012): Straightening out the screw-pines: A first step in understanding phylogenetic relationships within Pandanaceae. – Taxon, 61: 1010–1020. https://doi.org/10.1002/tax.615008

Callmander, M. W., Chassot, P., Küpfer, P., Lowry II, P. P. (2003): Recognition of *Martellidendron*, a new genus of Pandanaceae, and its biogeographic implications. – Taxon, 52: 747–762. https://doi.org/10.2307/4135547

Callmander, M. W., Lowry II, P. P., Forest, F., Devey, D. S., Beentje, H., Buerki, S. (2012): *Benstonea* Callm. et Buerki (Pandanaceae): Characterization, circumscription, and distribution of a new genus of Screw-Pines, with a synopsis of accepted species. – Candollea, 67: 323–345. https://doi.org/10.15553/c2012v672a12

Chandler, M. E. J. (1961): The Lower Tertiary Floras of Southern England. I. Palaeocene Floras. London Clay Flora (Supplement). – British Museum (Natural History), London, 354 pp. https://doi.org/10.5962/bhl.title.110079

Chesters, K. I. M. (1957): The Miocene flora of Rusinga Island, Lake Victoria, Kenya. – Palaeontographica, Abt. B., Paläophytologie, 101: 30–71.

Collinson, M. E., Manchester, S. R., Wilde, V. (2012): Fossil fruits and seeds of the middle Eocene Messel Biota, Germany. – Abhandlungen der Senckenberg Gesellschaft für Naturforschung, 570: 1–251.

Dahlgren, R. M. T., Clifford, H. T., Yeo, P. F. (1985): The Families of the Monocotyledons. –Springer-Verlag, Berlin, 520 pp. https://doi.org/10.1007/978-3-642-61663-1

Davies-Vollum, K. S., Wing, S. L. (1998): Sedimentological, taphonomic and climatic as aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming). – Palaios, 13: 28–40. https://doi.org/10.2307/3515279

Dawson, M. (1980): Paleontology and geology of the Badwater Creek area, central Wyoming. Part 20. The Late Eocene Creodonta and Carnivora. – Annals of the Carnegie Museum of Natural History, 49: 79–91.

De Wilde, J. J. O., Duyfjes, B. (2016): A conspectus of *Alangium* Lam. sect. *Alangium* (Alangiaceae). – Thai Forest Bulletin, Botany, 44: 74–87. https://doi.org/10.20531/tfb.2016.44.1.12

Del Rio, C., Stull, G. W., De Franceschi, D. (2019): New species of *Iodes* fruits (Icacinaceae) from the early Eocene Le Quesnoy locality, Oise, France. – Review of Palaeobotany and Palynology, 262: 60–71. https://doi.org/10.1016/j.revpalbo.2018.12.005

Dorf, E. (1938): Upper Cretaceous Floras of the Rocky Mountain Region. I: Stratigraphy and Paleontology of the Fox Hills and lower Medicine Bow Formations of southern Wyoming and Northwestern Colorado. – Carnegie Institute of Washington, Contributions to Paleontology, 508: 1–78.

Dorofeev, P. I. (1982): Vidy, ustanovlennye po endokarpiyam. *Celtis* i *Aphnanthe* [Species determined from endocarps. *Celtis* and *Aphnanthe*]. – In: Takhtajan, A., Zhilin, S. (eds), Magnoliophya Fossilia URSS., vol. 2, Ulmaceae – Betulaceae. Nauka, Leningrad, pp. 22–24. (in Russian)

Elsik, W. C. (1968): Palynology of a Paleocene Rockdale Lignite, Milam County, Texas. I. Morphology and taxonomy. – Pollen and Spores, 10: 263–314.

Emry, R. J. (1975): Revised Tertiary stratigraphy and paleontology of the western Beaver Divide, Fremont County, Wyoming. – Smithsonian Contributions to Paleobiology, 25: 1–20. https://doi.org/10.5479/si.00810266.25.1

Evernden, J. F., Savage, D. E., Curtis, G. H., James, G. T. (1964): Potassium-argon dates and the Cenozoic mammalian chronology of North America. – American Journal of Science, 262: 145–198. https://doi.org/10.2475/ajs.262.2.145

Eyde, R. H. (1963): Morphological and paleobotanical studies of the Nyssaceae, I. A survey of the modern species and their fruits. – Journal of the Arnold Arboretum, 44: 1–54. https://doi.org/10.5962/p.185657

Eyde, R. H., Bartlett, A., Barghoorn, E. S. (1969): Fossil record of *Alangium*. – Bulletin of the Torrey Botanical Club, 96: 288–314. https://doi.org/10.2307/2483735

Fairon-Demaret, M., Smith T. (2002): Fruits and seeds from the Tienen Formation at Dormal, Palaeocene-Eocene transition in eastern Belgium. – Review of Palaeobotany and Palynology, 122: 47–62. https://doi.org/10.1016/S0034-6667(02)00103-3

Fierro, D., Jones J. (1990): A fossil dicotyledonous wood from the middle upper Eocene of Wyoming. – In: Program with Abstracts of Papers to be Presented at the Annual Meetings of the Botanical Society of America with Other Affiliated Societies and the Association for Tropical Biology at Richmond, Virginia, August 5th – 9th 1990. American Journal of Botany, 77: 86.

Gallaher, T., Callmander, M. W., Buerki, S., Keeley, S. C. (2015): A long distance dispersal hypothesis for the Pandanaceae and the origins of the *Pandanus tectorius* complex. – Molecular Phylogenetics and Evolution, 83: 20–32. https://doi.org/10.1016/j.ympev.2014.11.002

Gazin, C. L. (1971): Paleocene primates from the Shotgun Member of the Fort Union Formation in the Wind River Basin, Wyoming. – Proceedings of the Biological Society of Washington, 84: 13–38.

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

Geolex: Geologic unit Wagon Bed. –https://ngmdb.usgs.gov/Geolex/UnitRefs/WagonBedRefs_11021.html [(accessed 23, 09 2021)]

Gingerich, P. (1989): New earliest Wasatchian mammalian fauna from the Eocene of Northwestern Wyoming: composition and diversity in a rarely sampled high-flood-plain assemblage. – University of Michigan Papers on Paleontology, 28: 1–97.

Greenwood, D. R., Wing, S. L. (1995): Eocene Continental climates and longitudinal temperature gradients. – Geology, 23: 1044–1048.
https://doi.org/10.1130/0091-7613(1995)023<1044:ECCALT>2.3.CO;2

Gunnell, G. F., Zonneveld, J.-P., Bartels, W. S. (2016): Stratigraphy, mammalian paleontology, paleoecology and age correlation of the Wasatch Formation, Fossil Butte National Monument, Wyoming. – Journal of Paleontology, 90: 981–1011.
https://doi.org/10.1017/jpa.2016.100

Gregor, H.-J., Goth, K. (1979): Erster Nachweis der Gattung *Canarium* Stickman 1759 (Burseraceae) im europäischen Alttertiär. – Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie), 47: 1–15.

Hamersma, A., Hererra, F., Wurdack, K., Manchester, S. R. (2022): *Belenocarpa tertiara* (Berry) gen. et comb. nov. (Euphorbiaceae): fossil fruits with carunculate seeds from the Oligocene of Peru. – International Journal of Plant Sciences, 183(4): 296–306.
https://doi.org/10.1086/718830

Han, M., Manchester, S. R., Wu, Y., Jin, J., Quan, C. (2018): Fossil fruits of *Canarium* (Burseraceae) from Eastern Asia and their implications for phytogeographical history. – Journal of Systematic Palaeontology, 16: 841–852.
https://doi.org/10.1080/14772019.2017.1349624

Harper, J. L., Lovell, P. H., Moore, K. G. (1970): The shapes and sizes of seeds. – Annual Review of Ecology and Systematics, 1: 327–356.
https://doi.org/10.1146/annurev.es.01.110170.001551

Herrera, F., Mitchell, J. D., Pell, S. K., Collinson, M. E., Daly, D. C., Manchester, S. R. (2018): Fruit morphology and anatomy of the Spondioid Anacardiaceae. – Botanical Review, 84: 315–393.
https://doi.org/10.1007/s12229-018-9201-1

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

Hill, A. W. (1933): The method of germination of seeds enclosed in a stony endocarp. – Annals of Botany, 47: 873–887.
https://doi.org/10.1093/oxfordjournals.aob.a090423

Hill, A. W. (1937): The method of germination of seeds enclosed in a stony endocarp. II. – Annals of Botany, new ser., 1: 239–256.
https://doi.org/10.1093/oxfordjournals.aob.a083466

Hotton, C. L., Lefingwell, H. A., Skvarla, J. J. (1994): Pollen ultrastructure and the fossil genus *Pandaniidites*. – In: Kurmann, M. H., Doyle, J. A. (eds), Ultrastructure of fossil spores and pollen. Royal Botanic Gardens, Kew, pp. 173–191.

Huegele, I., Manchester, S. R. (2019): Newly recognized diversity of fruits and seeds from the late Paleogene of Trinity County, Texas. – International Journal of Plant Sciences, 180: 681–708.
https://doi.org/10.1086/704358

Issa, N., Jones, J. (1990): Examination of a silicified wood (Ulmaceae?) from the Wagon Bed Formation of Wyoming. – In: Program with Abstracts of Papers to be Presented at the Annual Meetings of the Botanical Society of America with Other Affiliated Societies and the Association for Tropical Biology at Richmond, Virginia, August 5th – 9th 1990. American Journal of Botany, 77(6): 87–88.

Jacques, F. M. B. (2009): Survey of the Menispermaceae endocarps. – Adansonia, Sér. 3, 31: 47–87.
https://doi.org/10.5252/a2009n1a4

Jacques, F. M. B., De Franceschi, D. (2005): Endocarps of Menispermaceae from Le Quesnoy outcrop (Sparnacian facies, Lower Eocene, Paris Basin). – Review of Palaeobotany and Palynology, 135: 61–70.
https://doi.org/10.1016/j.revpalbo.2005.02.005

Jarzen, D. (1978): Some Maestrichtian palynomorphs and their phytogeographical and palaeoecological implications. – Palynology, 2: 29–38.
https://doi.org/10.1080/01916122.1978.9989163

Jarzen, D. (1983): The fossil record of the Pandanaceae. – Gardens' Bulletin of Singapore, 36: 163–175.

Keefer, W. R. (1961): Waltman Shale and Shotgun Members of Fort Union Formation (Paleocene) in Wind River Basin, Wyoming. – American Association of Petroleum Geologists Bulletin, 45: 1310–1323.
https://doi.org/10.1306/BC7436E3-16BE-11D7-8645000102C1865D

Keefer, W. R. (1965): Stratigraphy and geologic history of the uppermost Cretaceous, Paleocene and Lower Eocene rocks in the Wind River Basin, Wyoming. – U.S. Geological Survey Professional Paper, 495-A: 1–77.
https://doi.org/10.3133/pp495A

Keefer, W. R. (1970): Structural geology of the Wind River Basin, Wyoming. – U.S. Geological Survey Professional Paper, 495-D: 1–35.
https://doi.org/10.3133/pp495D

Kessler, P. J. A. (1993): Menispermaceae. – In: Kubitzki, K. (ed.), The Families and Genera of Vascular Plants. II. Flowering Plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families. Springer Verlag, Berlin, pp. 402–418.
https://doi.org/10.1007/978-3-662-02899-5_48

Krishtalka, L. (1978): Paleontology and geology of the Badwater Creek area, central Wyoming. Part 15. Review of the late Eocene primates from Wyoming and Utah, and the Plesitarsiiformes. – Annals of the Carnegie Museum of Natural History, 47: 335–360.

Krishtalka, L., Setoguchi, T. (1977): Paleontology and geology of the Badwater Creek area, central Wyoming. Part 13. The late Eocene Insectivora and Dermoptera. – Annals of the Carnegie Museum of Natural History, 46: 71–99.

Krishtalka, L., West, R. M., Black, C. C., Dawson, M. R., Flynn, J. J., Turnbull, W. D., Stucky, R. K., McKenna, M. C., Bown, T. M., Golz, D. J., Lillegraven, J. A. (1987): Eocene (Wasatchian through Duchesnean) biochronology of North America. – In: Woodburne, M. O. (ed.), Cenozoic Mammals of North America: Geochronology and Biostratigraphy. University of California Press, Berkeley, pp. 76–117.

Kvaček, J., Herman, A. B. (2004): Monocotyledons from the Early Campanian (Cretaceous) of Grünbach, Lower Austria. – Review of Palaeobotany and Palynology, 128: 323–353.
https://doi.org/10.1016/S0034-6667(03)00154-4

Lam, H. J. (1932): Beiträge zur morphologie der Burseraceae inbesondere der Canarieae. – Annales du Jardin Botanique de Buitenzorg, 42: 97–226.

Leenhouts, P. W. (1956): Burseraceae. – In: van Steenis, C. G. G. J. (ed.), Flora Malesiana, Ser. 1, vol. 5. P. Noordhoff Publishers, Groningen, pp. 209–296.

Leenhouts, P. W. (1959): Revision of the Burseraceae of the Malaysian area in the wider sense. X. *Canarium* Stickm. – Blumea, 9: 275–475.

Leffingwell, H. A. (1971): Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) Formations of the type Lance area, Wyoming. – Geological Society of America Special Paper, 127: 1–21.
https://doi.org/10.1130/SPE127-p1

Leopold, E. B., MacGinitie, H. D. (1972): Development and affinities of Tertiary floras in the Rocky Mountains. – In: Graham, A. (ed.), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, Amsterdam, pp. 147–200.

Leopold, E. B., Manchester, S., Meyer H. W. (2008): Phytogeography of the late Eocene Florissant flora reconsidered. – In: Meyer, H. W., Smith, D. M. (eds), Paleontology of the Upper Eocene Florissant Formation, Colorado. Geological Society of America Special Paper, 435: 53–70.
https://doi.org/10.1130/2008.2435(04)

Leroy, J. F. (1955): Étude sur les Juglandaceae. A la recherché d'une conception morphologique de la fleur femelle et du fruit. – Mémoires du Muséum National D'Histoire Naturelle, Serie B, Botanique, 6: 1–246.

Liu, Y.-C., Peng, H. (2009): *Mastixia microcarpa* (Mastixiaceae), a new species from Yunnan, China. – Annales Botanici Fennici, 46: 566–568.
https://doi.org/10.5735/085.046.0610

Love, J. D. (1970): Cenozoic geology of the Granite Mountains area, central Wyoming. – U.S. Geological Survey Professional Paper, 495-C: 1–154.
https://doi.org/10.3133/pp495C

Love, J. D., Leopold, E. G., Love, D. W. (1978): Eocene rocks, fossils and geologic history, Teton Range, northwestern Wyoming. – U.S. Geological Survey Professional Paper, 932-B: 1–38.
https://doi.org/10.3133/pp932B

Mabberley, D. J. (2008): Mabberley's Plant-Book, 3rd ed. – Cambridge University Press, Cambridge, 1019 pp.

MacGinitie, H. D. (1941): A middle Eocene flora from the central Sierra Nevada. – Carnegie Institution of Washington, Publications in Paleontology, 534: 1–178.

MacGinitie, H. D. (1974): An early middle Eocene flora from the Yellowstone-Absaroka volcanic province, northwestern Wind River Basin, Wyoming. – University of California Publications in Geological Sciences, 108: 1–103.

Mai, D. H. (1981): Der Formenkreis der Vietnam-Nuss (*Carya poilanei* (Chev.) Leroy in Europa. – Feddes Repertorium, 92: 339–385.
https://doi.org/10.1002/fedr.19810920502

Mai, D. H. (1993): On the extinct Mastixiaceae (Cornales) in Europe. – Geophytology, 23: 53–63.

Manchester, S. R. (1987): The fossil history of the Juglandaceae. – Monographs in Systematic Botany, Missouri Botanical Garden, 21: 1–137.
https://doi.org/10.5962/bhl.title.154222

Manchester, S. R. (1989): Systematics and fossil history of the Ulmaceae. – In: Crane, P. R., Blackmore, S. (eds), Evolution, Systematics, and Fossil History of the Hamamelidae, Volume 2: 'Higher' Hamamelidae (Systematics Association Special Volume 40B). Clarendon Press, Oxford, pp. 221–252.

Manchester, S. R. (1994): Fruits and seeds of the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. – Palaeontographica Americana, 58: 1–205.

Manchester, S. R. (1999): Biogeographical relationships of North American Tertiary floras. – Annals of the Missouri Botanical Garden, 86: 472–522.
https://doi.org/10.2307/2666183

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

Manchester, S. R., Akhmatiev, M. A., Kodrul, T. M. (2002): Leaves and fruits of *Celtis aspera* Newberry (comb. nov.) Celtidaceae from the Paleocene of North America and Eastern Asia. – International Journal of Plant Sciences, 163: 725–736.
https://doi.org/10.1086/341513

Manchester, S. R., Hermsen, E. J. (2001): Flowers, fruits, seeds and pollen of *Landeenia* gen. nov., an extinct Sapindalean genus from the Eocene of Wyoming. – American Journal of Botany, 87: 1909–1914.
https://doi.org/10.2307/2656842

Manchester, S. R., Judd, W. S., Handley, B. (2006): Foliage and fruits of early poplars (Salicaceae: *Populus*) from the Eocene of Utah, Colorado, and Wyoming. – International Journal of Plant Sciences, 167: 897–908.
https://doi.org/10.1086/503918

Manchester, S. R., McIntosh, W. C. (2007): Late Eocene silicified fruits and seeds from the John Day Formation near Post, Oregon. – PaleoBios, 27: 7–17.

Manchester, S. R., O'Leary, E. (2010): Distribution and identification of fin-winged fruits. – Botanical Review, 76: 1–82.
https://doi.org/10.1007/s12229-010-9041-0

Matthew, K. M. (1976): A revision of the genus *Mastixia* (Cornaceae). – Blumea, 23: 51–93.

Miki, S. (1938): On the change of flora of Japan since the upper Pliocene and the floral composition at the present. – Japanese Journal of Botany, 9: 213–251.

Mitchell, J. D., Daly, D. C., Pell, S. K., Randrianasolo, A. (2006): *Poupartiopsis* gen. nov. and its context in An-

acardiaceae classification. – Systematic Botany, 31: 337–348.
https://doi.org/10.1600/036364406777585757

Muller, J. (1981): Fossil pollen records of extant angiosperms. – Botanical Review, 47: 1–146.
https://doi.org/10.1007/BF02860537

Myers, J. A. (1990): A Bridgerian age flora from Del Mar, California; Master's Thesis. – MS, San Diego State University, San Diego, CA, USA, 164 pp. (available online: https://digitallibrary.sdsu.edu/islandora/object/sdsu%3A28053).

Pekarek, A., Marvin, R. F., Mehnert, H. H. (1974): K-Ar ages of the volcanics in the Rattlesnake Hills, central Wyoming. – Geology, 2: 282–285.
https://doi.org/10.1130/0091-7613(1974)2<283:KAOT-VI>2.0.CO;2

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

Prothero, D. R., Sanchez, F. (2004): Magnetic stratigraphy of the middle to upper Eocene section at Beaver Divide, Fremont County, central Wyoming. – Bulletin of the New Mexico Museum of Natural History and Science, 26: 151–154.

Rankin, B. D., Stockey, R. A., Beard, G. (2008): Fruits of Icacinaceae from the Eocene Appian Way locality of Vancouver Island, British Columbia. – International Journal of Plant Sciences, 169: 305–314.
https://doi.org/10.1086/523876

Reid, E. M., Chandler, M. E. J. (1933): The London Clay flora. – British Museum (Natural History), London, 561 pp.
https://doi.org/10.5962/bhl.title.110147

Rozefelds, A., Dettmann, M., Clifford, T., Hocknull, S., Newman, N., Godthelp, H., Hand, S., Archer, A. (2015): Traditional and computed tomographic (CT) techniques link modern and Cenozoic fruits of *Pleiogynium* (Anacardiaceae) from Australia. – Alcheringa, 39: 24–39.
https://doi.org/10.1080/03115518.2014.951916

Salami, D., Jones, J. (1990): A silicified fagaceous wood from the Paleogene of Wyoming. – In: Program with Abstracts of Papers to be Presented at the Annual Meetings of the Botanical Society of America with Other Affiliated Societies and the Association for Tropical Biology at Richmond, Virginia, August 5th – 9th 1990. American Journal of Botany, 77(6): 98.

Sattarian, A., van der Maesen L. J. G. (2006): Endocarp morphology of African *Celtis*. – Blumea, 51: 389–397.
https://doi.org/10.3767/000651906X622337

Scott, R. A. (1954): Fossil fruits and seeds from the Eocene Clarno Formation. – Palaeontographica, Abt. B., Paläophytologie, 96: 66–97.

Scott, R. A. (1956): Evolution of some endocarpal features in the tribe Tinosporeae (Menispermaceae). – Evolution, 10: 74–81.
https://doi.org/10.1111/j.1558-5646.1956.tb02831.x

Stockey, R. A., Hoffman, G. L., Rothwell, G. W. (1997a): The Fossil Monocot *Limnobiophyllum scutatum*: Resolving the phylogeny of Lemnaceae. – American Journal of Botany, 84: 355–368.
https://doi.org/10.2307/2446009

Stockey, R. A., LePage, B. L., Pigg, K. B. (1997b): Permineralized fruits of *Diplopanax* (Cornaceae, Mastixioideae) from the middle Eocene Princeton Chert of Columbia. – Review of Palaeobotany and Palynology, 103: 223–234.
https://doi.org/10.1016/S0034-6667(98)00038-4

Stone, B. C., Huynh, K.-L., Poppendieck, H.-H. (1998): Pandanaceae. – In: Kubitzki, K. (ed.), The Families and Genera of Vascular Plants, vol. III. Flowering Plants. Monocotyledons. Lilianae (Except Orchidaceae). Springer Verlag, Berlin, pp. 397–404.
https://doi.org/10.1007/978-3-662-03533-7_47

Strait, S. G., Holroyd, P. A., Denvir, C. A., Rankin, B. D. (2016): Early Eocene (Wasatchian) rodent assemblages from the Washakie Basin, Wyoming. – PaleoBios, 33: 1–28.
https://doi.org/10.5070/P9331029986

Stull, G. W., Adams, N. F., Manchester, S. R, Sykes, D., Collinson, M. E. (2016): Revision of Icacinaceae from the Early Eocene London Clay flora based on X-ray micro-CT. – Botany, 94: 713–745.
https://doi.org/10.1139/cjb-2016-0063

Tardieu-Blot, M.-L. (1962): Anacardiacées.– In: Aubréville, A. (ed.), Flore du Cambodge, du Laos et du Vietnam, Fasc. 2. Muséum National d'Histoire Naturelle, Paris, pp. 67–200.

Tiffney, B. H. (1984): Seed size, dispersal syndromes and the rise of the angiosperms: evidence and hypothesis. – Annals of the Missouri Botanical Garden, 71: 551–576.
https://doi.org/10.2307/2399037

Tiffney, B. H. (1985a): Perspectives on the origins of the floristic similarity between Eastern Asia and Eastern North America. – Journal of the Arnold Arboretum, 66: 73–94.
https://doi.org/10.5962/bhl.part.13179

Tiffney, B. H. (1985b): The Eocene North Atlantic land bridge: Its importance in Tertiary and modern phytogeography of the Northern Hemisphere. – Journal of the Arnold Arboretum, 66: 243–273.
https://doi.org/10.5962/bhl.part.13183

Tiffney, B. H. (1999): Fossil fruit and seed flora from the Early Eocene Fisher/Sullivan site. – In: Weems R. J, Grimsley, G. J. (eds), Early Eocene Vertebrates and Plants from the Fisher/Sullivan Site (Nanjemoy Formation) Stafford County, Virginia. Virginia Division of Mineral Resources Publication, 152: 139–159.

Tiffney, B. H., Haggard, C. (1996): Fruits of Mastixioideae (Cornaceae) from the Paleogene of western North America. – Review of Palaeobotany and Palynology, 92: 29–54.
https://doi.org/10.1016/0034-6667(96)00104-2

Todzia, C. A. (1993): Ulmaceae. – In: Kubitzki, K. (ed.), The Families and Genera of Vascular Plants. II. Flowering Plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families. Springer Verlag, Berlin, pp. 603–611.
https://doi.org/10.1007/978-3-662-02899-5_75

Van Houten, F. B. (1964): Tertiary geology of the Beaver Rim area, Fremont and Natrona Counties, Wyoming. – U.S. Geological Survey Bulletin, 1164: 1–99.

Upchurch, G. R., Mack, G. H. (1998): Latest Cretaceous leaf megafloras from the Jose Creek Member, McRae Formation of New Mexico. – In: Mack, G. H., Austin, G. S., Barker, J. M. (eds), Las Cruces Country II. New Mexico

Geological Society 49th Annual Fall Field Conference Guidebook, pp. 209–222.

Wannan, B. S., Quinn, C. (1990): Pericarp structure and generic affinities in the Anacardiaceae. – Botanical Journal of the Linnean Society, 102: 225–252.
https://doi.org/10.1111/j.1095-8339.1990.tb01878.x

Wilf, P. (2000): Late Paleocene-early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. – Geological Society of America Bulletin, 112: 292–307.
https://doi.org/10.1130/0016-7606(2000)112<292:LPECCI>2.0.CO;2

Wilkinson, H. P. (1968): *Dracontomelon costatum* Blume (Anacardiaceae), an augmented description. – Journal of Natural History, 2: 39–46.
https://doi.org/10.1080/00222936800770611

Wing, S. L., Alroy, J., Hickey, L. J. (1995): Plant and mammal diversity in the Paleocene to Early Eocene of the Bighorn Basin. – Palaeogeography, Palaeoclimatology and Palaeoecology, 115: 117–155.
https://doi.org/10.1016/0031-0182(94)00109-L

Wing, S. L., Greenwood, D. R. (1993): Fossils and fossil climates: The case for equable continental interiors in the Eocene. – Philosophical Transactions, Royal Society of London, B, 341: 243–252.
https://doi.org/10.1098/rstb.1993.0109

Wolfe, J. A. (1971): Tertiary climatic fluctuations and methods of analysis of Tertiary floras. – Palaeogeography, Palaeoclimatology, Palaeoecology, 9: 27–57.
https://doi.org/10.1016/0031-0182(71)90016-2

Wolfe, J. A. (1977): Paleogene floras from the Gulf of Alaska region. – U.S. Geological Survey Professional Paper, 997: 1–108.
https://doi.org/10.3133/pp997

Wolfe, J. A. (1978): A Paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. – American Scientist, 66: 694–703.

Wolfe, J. A. (1987): An overview of the origins of the modern vegetation and flora of the northern Rocky Mountains. – Annals of the Missouri Botanical Garden, 74: 785–803.
https://doi.org/10.2307/2399450

Zhang, W.-P., Bai, W.-N., Zhang, D.-Y. (2022): The rediscovery of *Carya poilanei* (Juglandaceae) after 80 years reveals a new record from China. – Phytokeys, 188: 73–92.
https://doi.org/10.3897/phytokeys.188.77242

Zhou, W., Xiang, Q. Y., Wen, J. (2020): Phylogenomics, biogeography, and evolution of morphology and ecological niche of the eastern Asian-eastern North American *Nyssa* (Nyssaceae). – Journal of Systematics and Evolution, 58: 571–603.
https://doi.org/10.1111/jse.12599