



DIVERSE FRUITS AND SEEDS OF THE MID-EOCENE KISHENEHN FORMATION, NORTHWESTERN MONTANA, USA, AND THEIR IMPLICATIONS FOR BIOGEOGRAPHY

MACKENZIE A. SMITH^{1*}, DALE E. GREENWALT², STEVEN R. MANCHESTER¹

¹ Florida Museum of Natural History, 1659 Museum Rd, Gainesville, FL 32611 USA; e-mails: mackenziesmith@ufl.edu, steven@flmnh.ufl.edu.

² Department of Paleobiology, NMNH, Smithsonian Institution, P.O. Box 37012 MRC 121, Washington, D.C. 20013 USA; e-mail: GreenwaltD@si.edu.

*corresponding author

Smith, M. A., Greenwalt, D. E., Manchester, S. R. (2023): Diverse fruits and seeds of the mid-Eocene Kishenehn Formation, northwestern Montana, USA, and their implications for biogeography. – *Fossil Imprint*, 79(1): 37–88, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Lacustrine shales of the Kishenehn Formation of northwestern Montana provide an important window to the local mid-Eocene (Lutetian) ecosystem including evidence from insects, molluscs, vertebrates and plants. However, little has been published on the macrofossils flora, which includes abundant compressed fruits and seeds as well as foliage. Here we provide a preliminary survey, with particular attention to reproductive remains from the Middle Fork Region. Identified families include Equisetaceae, Cupressaceae, Pinaceae, Betulaceae, Brassicaceae, Cercidiphyllaceae, Eucommiaceae, Juglandaceae, Oleaceae, Platanaceae, Rutaceae, Salicaceae, Sapindaceae, Simaroubaceae and Ulmaceae. With at least 107 entities, this is among the most diverse lacustrine megafossil floras in North America. This flora shares elements with the early to mid-Eocene Green River Parachute Creek Member flora of Colorado and Utah, the Thunder Mountain flora of Idaho and the Okanogan Highland floras of British Columbia and Republic, Washington, as well as some with the late Eocene Ruby flora of Montana. We estimate the mean annual temperature to have been between 8.91 and 12.10 °C and mean annual precipitation to have been between 945 and 1,204 mm using the Bioclimatic Analysis/Mutual Climate Range Technique. This summary of floral elements complements the faunal record of the Kishenehn Formation and fills a gap in prior knowledge of the paleofloristic distributions.

Key words: fossil plants, paleoclimate, Lutetian, shale, Lemnoideae, Brassicaceae

Received: March 3, 2023 | Accepted: August 8, 2023 | Issued: November 7, 2023

Introduction

The Eocene flora of western North America has been documented from many locations across the United States and Canada (reviewed in Wing 1987, Dillhoff et al. 2005, Greenwood et al. 2005, 2016, DeVore and Pigg 2010, Pigg and DeVore 2016, Lowe et al. 2018). Megafossils deposited in lake sediments have provided important insights into the climate and biogeographic relationships. In the Rocky Mountain region, the early and middle Eocene sediments of the Green River Formation have been particularly informative (reviewed by MacGinitie 1969, Wing 1987). The Kishenehn flora, collected from oil shales and siltstone near the southern border of Glacier National Park in northwestern Montana, along the Middle Fork of the Flathead River represents the northernmost Eocene site sampled from the United States Rocky Mountain region.

Lacustrine shales of the Kishenehn Formation in northwestern Montana are perhaps best known for their rich insect fauna and are regarded as a potential Conservat

Lagerstätte (Harbach and Greenwalt 2012, Greenwalt and Labandeira 2013, Greenwalt et al. 2013, 2014, 2016, 2019) that includes 15 orders dominated by the families Chironomidae (Diptera) and Corixidae (Hemiptera) (Greenwalt et al. 2015). In particular, the dipterans are incredibly diverse, represented by 21 different families with more species to be described (Greenwalt et al. 2019). These insects are unusually well preserved due to the presence of microbial mats which trapped the insects presumably in the spring and/or summer months (Greenwalt et al. 2015). The depth of the lake or fluvial delta is up for debate because there is conflicting evidence supporting both shallow nearshore and deep offshore environment (see Greenwalt et al. 2015).

Diverse freshwater molluscs have been recognized, comprising 37 terrestrial and 25 aquatic species representing tropical, subtropical/semi-arid and warm temperate environments that likely arose from the 2,000+ m elevational gradient to the east (Pierce and Constenius 2001, 2014). Several of the nearest living relatives of

these molluscan taxa can be found in South and Central America and the southeastern and southwestern US (Pierce and Constenius 2001, 2014). Twenty-six mammalian taxa are recognized from the Kishenehn Formation's mudstone and sandstone layers of the Coal Creek Member, ranging from multituberculates to titanotheres (Dawson and Constenius 2018). There are numerous scansorial species, indicating a wooded environment (Dawson and Constenius 2018). Several taxa including *Stockia* (Order Primates), *Tarkadectes* (Order Primates), Ischyromyidae (Order Rodenta), and *Amyrnodon* (Order Perissodactyla) show evidence of the biotic interchange between North America and Asia (Dawson and Constenius 2018). The low diversity of the Orders Carnivora and Artiodactyla may be reflective of both temporal (i.e., these orders might not have been abundant at this time) and ecological conditions (Dawson and Constenius 2018).

In addition, the same deposits include abundant plant remains in the form of leaves, fruits, and seeds. Here we present an overview of the fruit and seed assemblage from the Kishenehn flora as a basis for taxonomic and paleoecological comparison with other Eocene floras located to the south, west and north. We also present a few of the vegetative remains, e.g., *Equisetum*, conifers, *Alnus* and *Ulmus* that were identified in this initial investigation of the collections. We compare the Kishenehn ecosystem to that of the early to middle Eocene Green River Formation of Wyoming, Utah and Colorado as well as various early and mid-Eocene localities of Washington and British Columbia.

This analysis of the megafossil composition of the Kishenehn flora supplements prior palynological research on sediments of the same formation in Canada (Hopkins and Sweet 1976, Tshudy and Nichols cited in Constenius et al. 1989) to provide a fuller understanding of the vegetation that supported the diverse insect fauna in the same shales. Palynomorphs include lycopods, ferns, conifers, aquatic angiosperms such as *Typha* and *Nuphar*, wind-pollinated angiosperms such as Salicaceae, Betulaceae, Juglandaceae, Fagaceae and animal-pollinated taxa such as Onagraceae and Loranthaceae (Hopkins and Sweet 1976). For this study we examined 227 plant megafossil specimens (mostly reproductive structures) of which 158 specimens represent probably 51 biological species with the remainder comprising 45 fossil species. Over 30 reproductive and 20 foliage types remain to be described. We also estimate the paleoclimate using the flora.

Materials and Methods

The basin in which the Kishenehn Formation accumulated is a half-graben caused by crustal expansion along the Roosevelt and Nyack Faults (Dawson and Constenius 2018). The specimens investigated here were recovered from oil shale, siltstone and sandstone exposures adjacent to the highway and railroad about 25 km southeast of the town of West Glacier, west of the Lewis Mountains and thrust, and east of the Flathead Mountain Range and thrust, and east of the Flathead Mountains (Text-fig. 1). This exposure is located between Paola and Coal Creeks along the Middle Fork of the Flathead River and are a part of the

Coal Creek Member.

Ages estimates for the middle sequence of the Coal Creek Member are 46.2 ± 0.4 Ma based on $^{40}\text{Ar}/^{39}\text{Ar}$ analysis and 43.5 ± 4.9 Ma based on fission-track analysis, corresponding to the Lutetian stage of the Eocene (Constenius 1996). Pollen, mammal teeth and mollusks support these ages (Constenius et al. 1989, Pierce and Constenius 2001, 2014, Harbach and Greenwalt 2012, Dawson and Constenius 2018). These dates coincide with the Challis Magmatic Episode (Dawson and Constenius 2018).

To reveal fossils on the oil shale in the field, shale fragments were rinsed and gently rubbed with fingers in a nearby stream to remove obscuring matter, thereby improving contrast, and making them more readily visible. This does not harm the fossils – likely because of the encapsulating microbial layer on the shale (Greenwalt et al. 2014). Adjacent sandstone horizons containing abundant leaves such as *Macginitiea* (Constenius et al. 1989: fig. 2) are not included in this treatment but will be addressed in a future study as they come from a different depositional environment.

For this investigation, we studied specimens collected under the auspices of the United States Geological Survey in 1953 by C. E. Erdmann, V. K. Koskinen and R. Schmidt at USGS locality 9099 and deposited at the United States National Natural History Museum/Smithsonian (USNM), by D. E. Greenwalt from various localities, deposited at USNM, and by K. Constenius from various localities, deposited at the Denver Museum of Nature and Science (DMNH). Collections were made from 11 localities: Brown's Hole, Dakin, Deep Ford, Disbrow Creek, Iron Pole, Park, Pisces, Spring, Stanton Creek, and Tunnel Creek all near 48.2° N, 113.4° W, and Coal Creek near 48.3° N, 113.4° W. Specific locality data are on file at USNM. Identifications were made through comparison with other fossil floras and extant taxa.

For enhanced contrast, smaller specimens were studied with a dissecting microscope (Olympus SZX12 microscope equipped with a Q-Color5 Olympus DPS25 camera) and photographed while immersed in 95% ethanol. Larger specimens were photographed either dry or immersed in ethanol, with a copy stand using a Canon Rebel 450D SLR or Canon EOS 50D camera with a EFS 60 macrolens. Oblique lighting was provided by a pair of incandescent lamps.

Paleoclimate

We estimated 14 paleoclimate variables using the Bioclimatic Analysis/Mutual Climate Range Technique (BA/MCRT), a coexistence approach that excludes the 10th and 90th percentile of total tolerance ranges from the taxa (Kotthoff et al. 2014). Those 14 variables were as follows: Mean Annual Temperature, Maximum Temperature of Warmest Month, Minimum Temperature of Coldest Month, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Mean Annual Precipitation, Precipitation of Wettest Month, Precipitation of Driest Month, Precipitation of Wettest Quarter, Precipitation of Driest Quarter, Precipitation of Warmest Quarter and Precipitation of Coldest Quarter. Because there



Text-fig. 1. a: Map of Montana with location of fossil sites indicated by arrow. **b:** Aerial view, looking west, of Kishenehn shale exposures with localities along railroad cut and highway cuts along the Middle Fork of the Flathead River. Google Earth imagery. **c:** Exposure of fossiliferous shale along railroad cut, looking south. Creek, in foreground, used for washing away the obscuring dirty film on specimens. **d:** Shale outcrop south of creek.

were taxa with unknown climatic tolerances, uncertainties were not calculated (Liang et al. 2003). GPS coordinates from present-day occurrences including both human and machine observation, were downloaded for every identifiable genus (and *Chilopsis* plus *Catalpa* for subfamily Catalpae) from the Global Biodiversity Information Facility

(GBIF 2023). We cross referenced the GPS coordinates with the bioclimatic variables in the WorldClim 2.1 database (Fick and Hijmans 2017). *Dipteronia* and *Boniodendron* (referred to as *Sinoradlkofera* in GBIF 2023) were removed from the analysis because of too few occurrence points. Data processing was performed in R using the *rgbif*, *dplyr*,

sp, raster, geodata, terra and ggplot2 packages (R Core Team 2022, Chamberlain et al. 2023, Wickham et al. 2023, Pebesma and Bivand 2005, Hijmans 2023, Hijmans et al. 2023, Wickham 2016). Assistance in coding was provided by ChatGPT 3.5 (OpenAI, version 3.5. <https://chat.openai.com>).

Systematic paleobotany

We recognize at least 107 botanical entities in the Kishenehn flora. Here we give an overview beginning with identified taxa and continuing with a numerical sequence of unidentified informal fossil taxa labeled KF1 to KF43 (KF for Kishenehn flora). Fossil taxa, outlined in Cleal and Thomas (2010), are fossils of plants that may be one or multiple organs of the same parent taxon, one or multiple modes of preservation of the same parent taxon or one or multiple life stages of the same parent taxon. Formal recognition of new fossil taxa requires a specific diagnosis (Cleal and Thomas 2010), however, our goal is to present an overview of the diversity rather than giving each fossil taxon a binomial. Specimen number prefixes used: USNM PAL – United States National Museum (Smithsonian Museum of Natural History, District of Columbia). DMNH EPI – Denver Museum of Nature and Science (Denver, Colorado), UF – Florida Museum of Natural History (Gainesville, Florida).

Order Equisetales BERCHT. et J.PRESL

Family Equisetaceae MICHX. ex DC.

Genus *Equisetum* L.

Equisetum sp.

Text-fig. 2a

Material. USNM PAL 620616.

Locality. Park.

Description. Stem 20.8 mm long and 2.2 mm wide; 3 nodes, 2 internodes; 5–6 leaves visible per node (estimate fully 10–12 leaves per node); basal leaves 2.9 mm long, 0.5 mm wide at base, apical leaves 5.1 mm long, 0.5 mm wide at base; sheath (excluding leaves) 4.0 mm long.

Remarks. *Equisetum* commonly grow in wet areas next to streams and ponds and is commonly preserved in the fossil record. The single specimen that we studied is noteworthy in the relatively elongate triangular leaves. Similar species include *Equisetum limosum*? L. which has longer internodes (Lesquereux 1878) and *E. winchesteri* BROWN from the Green River Formation of Wyoming and Colorado, but *E. winchesteri* is larger in width and has more leaves (Brown 1929). *Equisetum* is also recognized from the early Eocene Okanagan floras of British Columbia (Smith et al. 2012, Greenwood et al. 2016) and middle Eocene Thunder Mountain flora of Idaho (Axelrod 1998).

Order Pinales GOROZHANKIN

Coniferae 1

Text-fig. 2b

Material. USNM PAL 622297.

Locality. Disbrow Creek.

Description. Conifer leaf 19.3 mm long, 3.8 mm wide; petiole stout and rectangular, 0.8 mm long and 0.9 mm wide; leaf base asymmetrical, obtuse and rounded; apex not preserved or in matrix; midvein 0.6 mm; a pair of stomatal bands runs on both sides of the midvein, running parallel to it. Width of the stomatal bands varying between 0.2–0.3 mm.

Remarks. The affinities of this leaf remain is uncertain. Prominent stomatal bands can be found in leaves of Taxaceae (*Amentotaxus* PILG., *Cephalotaxus* SIEBOLD et ZUCC. ex ENDL., *Taxus* L.), Cupressaceae (*Sequoia* ENDL.) and Pinaceae (*Abies* L., *Pseudotsuga* CARRIÈRE and *Tsuga* (ENDL.) CARRIÈRE). However, these taxa have stomatal bands as wide or wider than the midvein, whereas our specimen has stomatal bands half of the width of the midvein. The leaf has narrower stomatal bands than those that have been recorded for *Amentotaxus* PILG. (eFloras 2008–2022). Modern *Amentotaxus* has leaves that are 20–115 mm long, 5–15 mm wide and with stomatal bands 1–2 mm wide (eFloras 2008–2022).

Coniferae 2

Text-fig. 2c

Material. USNM PAL 622081.

Locality. Disbrow Creek.

Description. Conifer leaf 9.9 mm long, 1.3 mm wide; base broken; apex asymmetrically rounded; midvein 0.3 mm wide.

Remarks. Gross morphology of this specimen does not provide enough information to determine whether this is the abaxial or adaxial side of the leaf. Cupressaceae, Pinaceae and Taxaceae are all possible affinities based on macromorphology.

Family Cupressaceae BARTLETT

Genus cf. *Metasequoia* MIKI

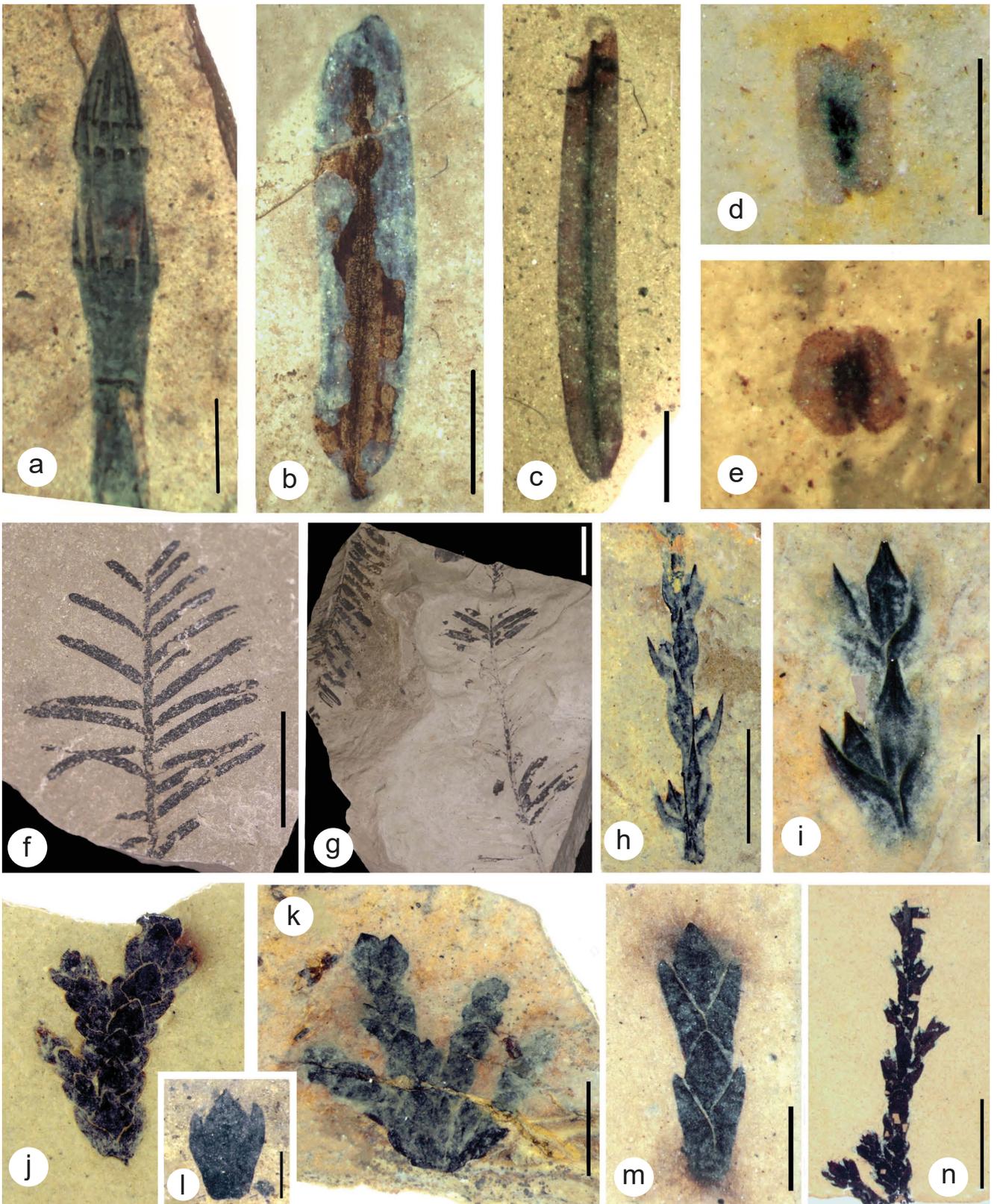
Text-fig. 2d, e

Material. USNM PAL 622101, 717666.

Locality. Dakin and Disbrow Creek.

Description. Winged seed round to rectangular with wings forming retuse connection at poles; 0.7–1.0 mm tall, 0.6 mm wide; seed body elliptical, in the center of the wings; polar ends of seed body in line with polar ends of wings; seed body 0.3–0.7 mm long, 0.2 mm wide.

Remarks. This seed bears a superficial resemblance to those of *Metasequoia* which has also been identified based on foliage from the Kishenehn Formation (Text-fig. 2f; USNM PAL 776571, 2g USNM PAL 776572). However, the extant *Metasequoia glyptostroboides* HU et W.C.CHEUNG has seeds that range between 4.2–5 mm long and 4.8–6 mm wide, about 4–5 times larger than the Kishenehn specimen (eFloras 2008–2022, Liu and Basinger 2009). Fossil *Metasequoia* seeds from other sites are also larger (e.g., 5–6 mm long and 6–7 mm wide; Falder et al. 1999). *Metasequoia* is a major component of the Early Eocene Falkland flora of British Columbia (Smith et al. 2012).



Text-fig. 2. *Equisetum* and conifers from the Kishenehn Formation. a: USNM PAL 620616 *Equisetum* sp. stem apex. Scale bar 3 mm. b: USNM PAL 622297 Coniferae 1. Scale bar 5 mm. c: USNM PAL 622081 Coniferae 2. Scale bar 2 mm. d: USNM PAL 717666 cf. *Metasequoia* sp. seed. Scale bar 1 mm. e: USNM PAL 622101 cf. *Metasequoia* sp. seed. Scale bar 1 mm. f: USNM PAL 776571 *Metasequoia* sp. twig showing opposite leaves. Scale bar 10 mm. g: USNM PAL 776572 *Metasequoia* sp. twigs. Scale bar 10 mm. h: USNM PAL 621667 *Juniperus* sp. leafy twig. Scale bar 5 mm. i: USNM PAL 722223 *Juniperus* sp. twig. Scale bar 2 mm. Scale bar 3 mm. j: USNM PAL 623467 unidentified Cupressoideae 1. Scale bar 3 mm. k: USNM PAL 620274 unidentified Cupressoidae 2 leaves. l: USNM PAL 620087 unidentified Cupressoideae 2. Scale bar 1 mm. m: USNM PAL 620184 unidentified Cupressoideae 3 shoot. Scale bar 2 mm. n: USNM PAL 621863 Cupressoideae 4 leafy twig. Scale bar 5 mm.

Genus *Juniperus* L.

***Juniperus* sp.**

Text-fig. 2h, i

Material. USNM PAL 621667, 722223.

Localities. Disbrow Creek and Tunnel Creek.

Description. Awl-shaped leaves 2.1–2.8 mm long, arranged helically around an axis 15.5 mm long and 1 mm wide; each leaf having a convex abaxial surface and concave adaxial surface, with a medial ridge extending from base to apex; three leaves apparently emerging from the axis at each node; wide leaf base and acute apex; ridge running down the center of each leaf from base to apex.

Remarks. *Juniperus* can have scale or needle leaves. These fossils possess needle leaves of the kind that generally occur on young trees or parts of the tree that are exposed to low light (Zhang et al. 2021). We also compared these leaves to those of *Cryptomeria* D.DON but their needle leaves continuously taper from their base to apex whereas *Juniperus* leaves become more acute part way up the to the leaf apex as in our fossils (pers. obs.). *Juniperus* is also known from the Oligocene Beaverhead Basin floras and considered a subhumid element (Wing 1987) and pollen with possible affinities to the genus has been reported from the early Eocene McAbee fossil beds in British Columbia (Lowe et al. 2018).

Subfamily Cupressoideae RICH. ex SWEET

Cupressoideae 1

Text-fig. 2j

Material. USNM PAL 623467.

Locality. Dakin.

Description. Scale leaves on an axis measuring 7.4 mm long and 1.7 mm wide; branchlets on one side, leaves decussate, 0.8–1.2 mm wide, wide bases and rounded acute apices 86°, distance between apices in the facial leaves (which is also the length of each leaf) ranges 0.9–1.1 mm; facial leaf apex covers junction of subsequent lateral leaves.

Remarks. Cupressoideae 1 differs from Cupressoideae 4 by having shorter leaves that are closely spaced and more rounded apices. Some foliage from cupressaceous genera can be indistinguishable, and we did not recover cones that would enable a more refined determination. It differs from Cupressoideae 2 by having leaf apices that overlap subsequent lateral leaf junctions. Leaves conforming to this description can be found in *Juniperus* L., *Thuja* L. and *Chamaecyparis* SPACH. Cupressoideae 1 may be the same as Cupressoideae 3. Leaves may be abscised in this specimen and not in Cupressoideae 3. Abscission can occur in genera like *Chamaecyparis*, so the facial leaves can either cover or not cover the junction of the subsequent lateral leaves (Kotyk et al. 2003).

Cupressoideae 2

Text-fig. 2k, l

Material. USNM PAL 620087, 620274.

Locality. Park.

Description. Scale leaves on axis measuring 8.0 mm long and 1.2 mm wide; branchlets sprawling; distance from facial leaf apices 1.7 mm; leaf height 1.4 mm, leaf width 0.9–1.0 mm; apex of facial leaf does not cover juncture of subsequent lateral leaves; leaf apex pointed to slightly rounded 99–110°; leaves are keeled.

Remarks. Cupressoideae 2 differs from Cupressoideae 1 and Cupressoideae 4 by having apices that do not cover the subsequent lateral leaf junctions, having obtuse leaf apices and by having keeled leaves. Cupressoideae 2 differs from Cupressoideae 3 by having shorter leaves (1.4 mm vs. 2.1 mm, respectively). This fossil cannot be placed confidently in a modern genus.

Cupressoideae 3

Text-fig. 2m

Material. USNM PAL 620184.

Locality. Park.

Description. Scaly leaf axis measuring 6.4 mm long, 1.8 mm wide at lateral leaf widest point; leaves 2.1 mm long, 1.1 mm wide; distance between facial leaf apices 2.6 mm; facial leaf apices do not cover subsequent lateral leaf junction; leaf apices rounded and acute 68°.

Remarks. Cupressoideae 3 differs from Cupressoideae 2 by having longer leaves (2.1 mm vs. 1.4 mm), that are non-keeled and acute apices. Cupressoideae 1 might be equivalent to Cupressoideae 3, with their different appearance due to abscission of leaves in the former. Abscission can occur in genera like *Chamaecyparis* such that the facial leaves can either cover or not cover the junction of the subsequent lateral leaves (Kotyk et al. 2003). Cupressoideae 3 differs from Cupressoideae 4 by having appressed leaf junctions instead of leaf junctions that flare outward. This fossil cannot be placed confidently in a modern genus.

Cupressoideae 4

Text-fig. 2n

Material. USNM PAL 621863.

Locality. Disbrow Creek.

Description. Scaly leaf axis measuring 17.3 mm long and 1.0 mm wide; branchlets opposite; leaves decussate, leaves triangular measuring 1.3 mm long with a pointed acute apex measuring between 59.0 and 88.5°; distance between apices on facial leaves 2.6–2.9 mm; apex of facial leaf covers junction of subsequent lateral leaves or may be below junction; lateral leaves separate on facial surface before angling outward.

Remarks. Cupressoideae 4 differs from Cupressoideae 1 and 2 by having longer leaves with pointed, rather than rounded apices and having longer internodes. Cupressaceae 4 differs from Cupressaceae 3 by having leaf junctions that flare outward instead of being appressed to the stem. The lateral leaves are not proportionally long enough to match those of *Tetraclinis* MAST. (Kvaček et al. 2000) and the facial leaves are more prominent than those of *Fokienia* A.HENRY et H.H.THOMAS (McIver 1992). *Mesocyparis* McIVER et

Table 1. Comparison of the four cupressaceous foliage types in the Kishenehn.

Taxon	Branching	Leaf width × height (mm)	Pointed or rounded apex	Facial leaves overlap junction of lateral leaves	Keeled leaves
Cupressoideae 1	Branchlets on one side?	0.8–1.2 × 0.9–1.1	Rounded	Yes	No
Cupressoideae 2	Sprawling	0.9–1.0 × 1.4	Pointed or rounded	No	Sometimes
Cupressoideae 3	Unknown	1.1 × 2.1	Rounded	No	No
Cupressoideae 4	Opposite	1.0 × 1.3	Pointed	Yes	Unknown

BASINGER has opposite instead of alternate branching (McIver et Basinger 1987, Kodrul et al. 2006). Alternate branching cupressaceous conifers including *Thuja*, *Chamaecyparis* and *Platyclusus* SPACH have lateral leaf apices that can be addressed to the side and are indistinguishable from one another (McIver and Basinger 1987, Wu et al. 2014). Thus, this fossil cannot be confidently placed into a genus.

Comments on the unknown Cupressoideae genera

The cupressoid foliage morphotypes are summarized in Tab. 1. There is a possibility that there may be fewer than four taxa because leaf size and shape can vary depending on location on the branch (McIver and Basinger 1987). Cupressaceous foliage is recognized from the early Eocene Falkland and McAbee floras of British Columbia. In particular, the genus *Chamaecyparis* was recognized from Falkland, McAbee (Dillhoff et al. 2005, Smith et al. 2012) and in the mid-Eocene Thunder Mountain flora by Axelrod (1998) and confirmed by Erwin and Schorn (2005).

Family Pinaceae F.RUDOLPHI

Genus *Abies* MILL.

Text-fig. 3a

Material. USNM PAL 621424.

Locality. Park.

Description. Winged seed linear, 11.7 mm long, 5.3 mm wide at widest; seed body elliptical 3.8 mm long, 2.3 mm wide oriented with long axis parallel to medial edge; seed body on proximal side of seed; seed body contains numerous, round resin vesicles; abmedial margin begins approximately one quarter of the way up seed body extending so widest area of wing is distal; distal edge straight; medial edge convex in distal quarter.

Remarks. Winged seeds with resin vesicles and with the wings widest in the distal half belong to *Abies* (Wolfe and Schorn 1990). *Abies* pollen is known from the early Eocene McAbee and Quilchena floras of British Columbia (Dillhoff et al. 2005, Lowe et al. 2018, Mathewes et al. 2016) and Yellowstone, Wyoming (Wing 1987). Macrofossils are known from the early Eocene McAbee and Falkland floras of British Columbia (Dillhoff et al. 2005, Lowe et al. 2018, Smith et al. 2012), Republic flora of Washington (Pigg et al. 2011), Green River Formation (Brown 1929) and Oligocene Beaverhead flora of Montana (Wing 1987). *Abies* is also recognized based on seeds and foliage from the mid-Eocene Thunder Mountain flora of Idaho (Axelrod 1998). Although the identity of some of the specimens that

were attributed to *Abies deweyensis* AXELROD, by Axelrod (1998) has been questioned due to disarticulated parts and a lack of diagnostic features (Erwin and Schorn 2005).

Genus *Larix* MILL.

Larix sp.

Text-fig. 3b

Material. USNM PAL 620036, 621991, 624288, 776559.

Localities. Dakin, Disbrow Creek and Park.

Description. Linear winged seed 6.2–14.0 mm long, 4.0–5.2 mm wide; widest portion of wing in proximal 1/3; seed body triangular with acute proximal point to elliptical and concave depression on surface; seed body at proximal end of seed, 2.3–3.3 mm long, 1.1–1.9 mm at widest point; distal edge of seed body rounded; wing linearly striated.

Remarks. Winged seeds with straight, rather than undulating striations, proximal seed bodies with distal portions of the seed bodies rounded and wings that are widest in the proximal half conform to *Larix* (Wolfe and Schorn 1990). The shape of the seeds resembles that of the modern taxa *Larix kaempferi* (LAMB.) CARRIÈRE, and *Larix decidua* var. *polonica* (RACIB. ex WÓYCICKI) OSTENF. et SYRACH (LePage and Basinger 1991).

Genus cf. *Larix* MILL.

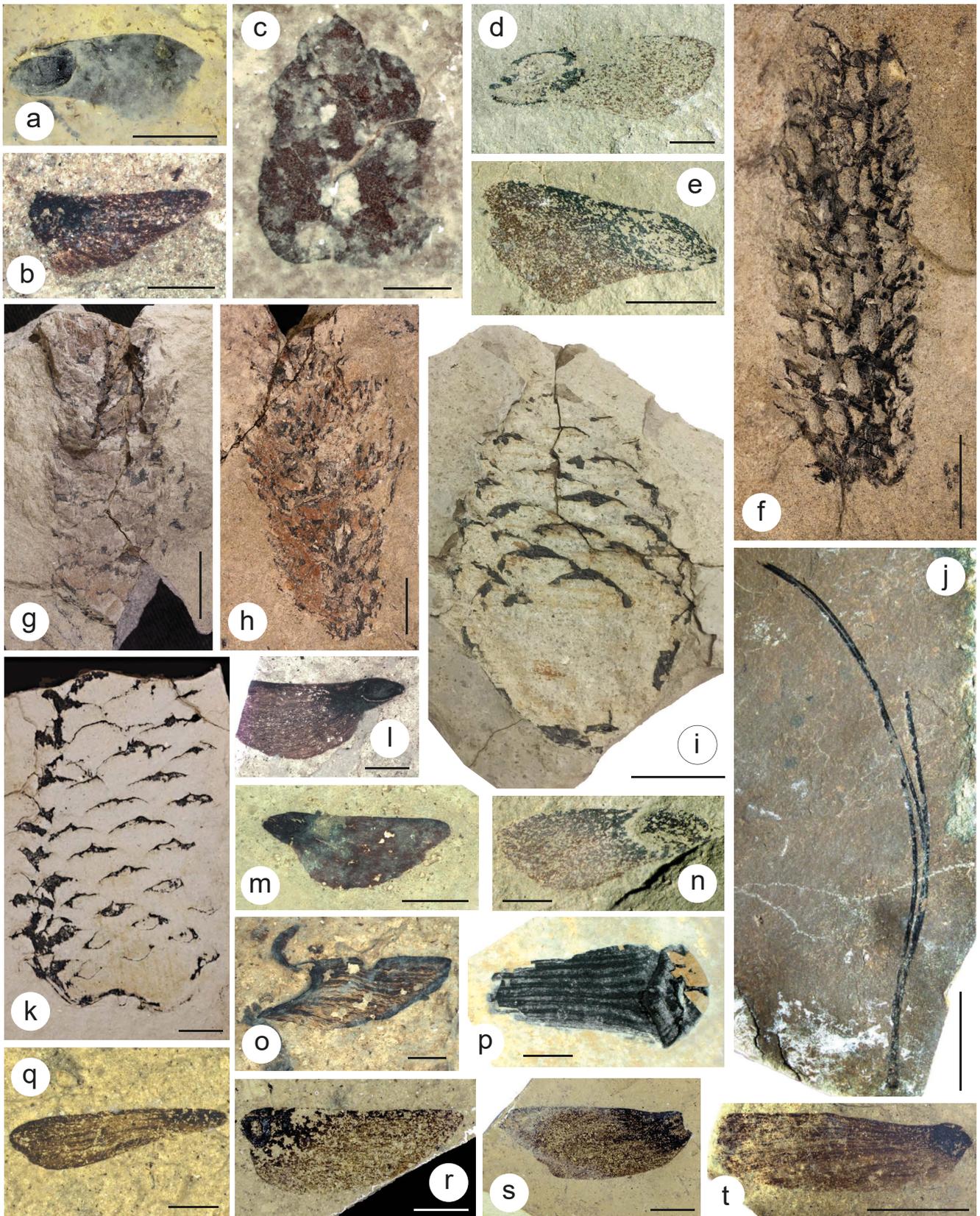
Text-fig. 3c

Material. USNM PAL 622093.

Locality. Disbrow Creek.

Description. Ovuliferous cone cylindrical 11.2 mm tall, 7.1 mm wide; scales helically arranged, about 4 rows; scales each have a pointed apex forming an angle of ~106°; scales 4.9 mm tall, 2.9 mm wide at base and 2.0 mm wide at apex.

Remarks. The extant *Larix laricina* (DU ROI) K.KOCH and *Picea mariana* BRITTON, STERNS et POGGENB. have relatively small seed cones (1–2 cm and 1.5–3.5 cm tall, respectively) (Parker 2021, Taylor 2021). Cone size in the fossil *Larix altoborealis* LEPAGE et BASINGER from the Eocene of Axel Heiberg, Nunavut, Canada ranges from 1.4–3.0 cm tall (LePage and Basinger 1991). *P. mariana* is slightly larger, has scales that are wider near the apex and has irregularly toothed scales (Taylor 2021). *L. laricina* cone scale apices are rounder than the fossil specimen but other *Larix* species, such as *L. gmelinii* LEDEB. ex GORDON, have



Text-fig. 3. Pinaceae from the Kishenehn Formation. a: USNM PAL 621424 *Abies* sp. seed. Scale bar 5 mm. b: USNM PAL 621991 *Larix* sp. winged seed. Scale bar 2 mm. c: USNM PAL 622093cf. *Larix* sp. ovuliferous cone. Scale bar 3 mm. d: USNM PAL 776558 *Picea* sp. 1 winged seed. Scale bar 3 mm. e: USNM PAL 776565 *Picea* sp. 2 seed. Scale bar 5 mm. f: USNM PAL 619964 Pinaceae Cone 1. Scale bar 1 cm. g: USNM PAL 776557 Pinaceae Cone 2. Scale bar 1 cm. h: USNM PAL 620025 Pinaceae Cone 3. Scale bar 1 cm. i: USNM PAL 776556 *Pinus* sp. C1. Scale bar 2 cm. j: DMNH EPL. 48178 *Pinus* sp. L1 3-leaf fascicle. Scale bar 2 cm. k: USNM PAL 776570 *Pinus* sp. C2 *Pinus* subg. *Strobus* female cone. Scale bar 1 cm. l: USNM PAL 621980 *Pinus* subg. *Strobus*, *Pinus* sp. S1 winged seed. Scale bar 3 mm. m: USNM PAL 622300 *Pinus* subg. *Strobus*, *Pinus* sp. S1 winged seed. Scale bar 5 mm. n: USNM PAL 776567 *Pinus* subg. *Strobus*, *Pinus* sp. S2 seed. Scale bar 2 mm. o: USNM PAL 620785 *Pinus* subg. *Strobus*, *Pinus* sp. S3 winged seed, with seed body disarticulated. Scale bar 2 mm. p: USNM PAL 626064 *Pinus* subg. *Pinus* female cone scale *Pinus* sp. C3. Scale

more obtusely pointed scale apices (eFlorAs 2008–2022). Thus, the fossil is being tentatively assigned to *Larix*.

Comments on fossil *Larix*

Larix pollen is known from the early Eocene McAbee flora of British Columbia (Lowe et al. 2018) and of Yellowstone, Wyoming (Wing 1987). *Larix* winged seeds from the mid-Eocene Thunder Mountain flora were initially identified as *Larix leonardii* AXELROD by Axelrod (1998) and later diagnosed as *Larix* sp. by Erwin and Schorn (2005) for a lack of diagnostic features. The majority of fossil *Larix* are distributed in higher latitudes in places like Canada, Alaska and Russia though they have also been reported in Poland (LePage and Basinger 1991, McIver and Basinger 1999). The presence of *Larix* in the Kishenehn flora may indicate locally cool conditions or that these fossils were transported from higher elevations.

Genus *Picea* MILL.

Picea sp. 1

Text-fig. 3d

Material. USNM PAL 619981, 776558.

Locality. Park.

Description. Linear winged seed 7.9–9.9 mm long, 3.6–4.6 mm wide at widest point; seed body elliptical to obovate, on proximal side of seed, 2.7–4.0 mm long, 2.1–2.4 mm wide, concave notch on proximal medial side; wing begins halfway down seed body along abmedial side and less than one quarter of the way to the seed body's terminus on the medial side; widest part of wing is just past the center more towards the distal end; medial and abmedial edges join in a smooth curve.

Picea sp. 2

Text-fig. 3e

Material. USNM PAL 776565, 776566.

Locality. Tunnel Creek.

Description. Winged seed linear 13.5–14.7 mm long, 6.2–6.9 mm wide; widest point of wing just distal of the halfway mark; wing encompasses most of seed body; seed body with concave notch on the proximal medial side; seed body obovate to elliptical 3.2–4.6 mm long, 1.6–2.0 mm wide.

Comments on fossil *Picea*

Picea seeds have a distinctive concave notch on the proximal medial side (Wolfe and Schorn 1990). *Picea* sp. 2 differs from *Picea* sp. 1 in being larger, with its widest point only slightly past the midpoint of the wing instead of more distal. The wing also encompasses more of the seed body. Pollen of *Picea* is recognized from the early Eocene Green River Formation (Wodehouse 1933, Nichols 2010), the Chuckanut Formation of Washington (Griggs 1970)

and the Quilchena flora of British Columbia (Mathewes et al. 2016). Macrofossils are known from the early Eocene Republic flora (Klondike Mountain Formation of Republic, Washington) (Pigg et al. 2011), McAbee and Falkland floras of British Columbia (Dillhoff et al. 2005, Smith et al. 2012), late Eocene Beaverhead Basin of Montana (DeVore and Pigg 2010) and Florissant Formation of Colorado (MacGinitie 1953), the Oligocene Creede Flora of Colorado (Wolfe and Schorn 1990) and Ruby River Basin of Montana (Becker 1961). Axelrod (1998) initially recognized *Picea coloradensis* AXELROD, *Picea deweyensis* AXELROD, and *Picea magna* AXELROD, from the mid-Eocene Thunder Mountain flora of Idaho. The specimens assigned to these species were subsequently identified as another genus, indeterminate, cf. *Picea* or *Picea* sp. by Erwin and Schorn (2005). The presence of *Picea* suggests microthermal conditions; these seeds may have come from the surrounding mountains around the basin (Dawson and Constenius 2018).

Pinaceae Cone 1

Text-fig. 3f

Material. USNM PAL 619964.

Locality. Dishbrow Creek.

Description. Structure cylindrical, 4.9 cm long, 1.6 cm wide, composed of helically arranged rectangular outlines; five rectangles wide and 9 rectangles tall, 0.4 cm tall, 0.1–0.3 cm wide, lateral extensions 0.2–0.3 cm.

Remarks. The rectangular outlines in the structure may be obscured leaf scars or cone scale scars. The lateral extensions may be remnants of bracts or scales or taphonomic degradation.

Pinaceae Cone 2

Text-fig. 3g

Material. USNM PAL 776557.

Locality. Dishbrow Creek.

Description. Ovuliferous cone cylindrical, 4.5 cm long, 2.1 cm wide, scales 1.4 mm long.

Pinaceae Cone 3

Text-fig. 3h

Material. USNM PAL 620025.

Locality. Park.

Description. Ovuliferous cone cylindrical, 5.5 cm long, 2.8 mm wide, at least 15 rows of scales, scales 1.3 cm long.

Comments on the three cones of uncertain affinity

All three cones appear to lack apophyses, so they are not *Pinus*. It is unclear whether they represent one or multiple species.

bar 1 cm. q: USNM PAL 622423 *Pinus* subg. *Pinus*, *Pinus* sp. S4 seed. Scale bar 2 mm. r: USNM PAL 625925 *Pinus* subg. *Pinus*, *Pinus* sp. S5 winged seed. Scale bar 2 mm. s: USNM PAL 625839 *Pinus* subg. *Pinus*, *Pinus* sp. S5 winged seed. Scale bar 3 mm. t: USNM PAL 622339 *Pinus* subg. *Pinus*, *Pinus* sp. S6 winged seed. Scale bar 5 mm.

Genus *Pinus* L.

***Pinus* sp. C1**

Text-fig. 3i

Material. USNM PAL 776556.

Locality. Tunnel Creek.

Description. Ovuliferous cone ovate; 5.9 cm tall, 1.2 cm wide; scales helical; apophysis narrow rhomboids 1.2–1.4 cm wide and 0.3 cm tall.

Remarks. Because the umbo is not clearly preserved, the fossil cannot be identified to subg. *Pinus* (dorsal umbo) or subg. *Strobis* (terminal umbo).

***Pinus* sp. L1**

Text-fig. 3j

Material. DMNH EPI.48178.

Locality. 6933.

Description. Three leaves in fascicle, fascicle 2.4 mm wide, leaves with sheath 126.2 mm long, leaves 0.8–1.3 mm wide.

Remarks. The preservation of the fossil does not allow us to determine if there was a sheath at the base of the fascicles. These are likely leaves from *Pinus* subg. *Pinus* because having three leaves per fascicle is a common trait in the group.

Subgenus *Strobis* LEMM.

***Pinus* sp. C2**

Text-fig. 3k

Material. USNM PAL 776570.

Locality. Coal Creek.

Description. Ovuliferous cone cylindrical; 7.7 cm tall, 4.6 cm wide; scale 1.7 cm long; at least 14 rows of scales, 3–4 scales wide, helically arranged; apophysis rhomboidal, 0.8–1.5 cm wide, 0.3–0.4 cm tall; umbo terminal; spine 0.1 cm long.

Remarks. The apophysis places this cone in the genus *Pinus* and the terminal umbo places this cone in the subgenus *Strobis*.

***Pinus* sp. S1**

Text-fig. 3l, m

Material. USNM PAL 621980, 622300.

Locality. Disbrow Creek.

Description. Winged seed linear, incomplete; 10.4–14.1 mm long, 4.4–5.0 mm wide at widest point; seed body on proximal side, obovate to elliptical, slightly detached from wing, distally rounded 2.2–3.2 mm long and 1.3–1.5 mm wide; admedial edge of wing begins a third of the way up the seed body and rapidly becomes larger at the end of the seed body's distal end; medial edge of wing straight to slightly concave; striations on wing slightly undulating, striations of similar thickness.

Remarks. *Pinus* subg. *Strobis* (also known as *Haploxylon*, the soft pines or white pines) have seed bodies

that can disarticulate, such that the fossil seeds of this subgenus are often missing the seed body. This fossil falls into Wolfe and Schorn's (1990) circumscription of atypical *Pinus* 4.

***Pinus* sp. S2**

Text-fig. 3n

Material. USNM PAL 620010, 776567.

Locality. Park.

Description. Winged seed, linear, 9.2–15.0 mm long, 3.3–8.0 mm wide at widest point; seed body elliptical on proximal end, 3.1–6.0 mm long, 1.7–6.6 mm wide; widest point of wing in distal half of wing; medial wing begins in distal quarter of seed body and abmedial wing edge begins halfway down seed body.

Remarks. The small size of the seed and small disarticulation between the seed body and the wing places this one in Wolfe and Schorn's (1990) atypical *Pinus* 4 group. The wing's widest point in the distal half of the seed differs from *Pinus* sp. S1 where it is in the proximal half.

***Pinus* sp. S3**

Text-fig. 3o

Material. 620785, 776563, 776568.

Locality. Park.

Description. Winged seed linear, 9.7 mm long, 4.0 mm wide; seed body on proximal side, elliptical, 3.5 mm long and 1.8 mm wide; base of seed body is tilted towards the abmedial side; wing widest in the middle; wing has bold, undulating striations.

Remarks. *Pinus* sp. S3 differs from *Pinus* sp. S1 and *Pinus* sp. S2 by having a seed body that is tilted towards the abmedial side and stronger striations on the wing. Because the seed body has completely disarticulated from the wing, we are unable to classify it based on Wolfe and Schorn's (1990) schema.

Subgenus *Pinus* L.

***Pinus* sp. C3**

Text-fig. 3p

Material. USNM PAL 626064.

Locality. Deep Ford.

Description. Cone scale 23.7 mm long; apophysis large, rhomboid, 7.1 mm tall and, 11.3 mm wide; umbo dorsal.

Remarks. *Pinus* subg. *Pinus* (also known as *Diploxylon*, the hard pines or yellow pines) have large, rhomboid apophyses and dorsal umbos.

***Pinus* sp. S4**

Text-fig. 3q

Material. USNM PAL 622423.

Locality. Disbrow Creek.

Description. Winged seed linear, 8.8 mm long, 2.2 mm wide at widest point; seed body elliptical, 1.7 mm

Table 2. Comparison of *Pinus* seeds found in the Kishenehn.

Taxon	Wolfe and Schorn (1990) classification	Seed size (length × width mm)	Seed body articulate	Seed body shape	Seed body size (length × width mm)	Widest part of wing	Striations
<i>Pinus</i> sp. S1	Atypical <i>Pinus</i> 4	10.4–14.1 × 4.4–5.0	No	Elliptical to obovate	2.2–3.2 × 1.3–1.5	Proximal half	Narrow
<i>Pinus</i> sp. S2	Atypical <i>Pinus</i> 4	9.2–15.0 × 3.3–8.0	No	Elliptical	3.1–6.0 × 1.7–6.6	Distal half	Narrow
<i>Pinus</i> sp. S3	Unknown	9.7 × 4.0	No	Elliptical	3.5 × 1.8	Middle	Bold
<i>Pinus</i> sp. S4	Atypical <i>Pinus</i> 1	8.8 × 2.2	Yes	Elliptical	1.7 × 0.7	Distal	Bold
<i>Pinus</i> sp. S5	Atypical <i>Pinus</i> 1	8.4–13.2 × 3.3–5.1	Yes	Elliptical	1.4–2.4 × 1.0–2.9	Proximal or constant	Narrow
<i>Pinus</i> sp. S6	Atypical <i>Pinus</i> 3	12.9–21.4 × 3.9–6.4	Yes	Circular	1.8–2.1	Constant	Bold

long, 0.7 mm wide; wing adnate to seed body on proximal side; seed body parallel to medial wing margin; admedial wing margin begins halfway down seed body and wing becomes widest in last quarter where distal margin forms an obtuse angle with the abmedial margin to connect with the medial margin; undulatory striations of various widths.

Remarks. Pine seeds with seed bodies adnate to the wing can occur in *Pinus* subg. *Pinus* (Wolfe and Schorn 1990). A *Diploxylon* pine seed with an admedial wing less than 1 cm and seed body less than 3 mm would place this fossil in Wolfe and Schorn's (1990) atypical *Pinus* 1.

***Pinus* sp. S5**

Text-fig. 3r, s

Material. USNM PAL 621289, 625839, 625925, 776560, 776562, 776564.

Localities. Iron Pole, Park and Stanton Creek.

Description. Winged seed linear 8.4–13.2 mm long, 3.3–5.1 mm wide; seed body circular to elliptical, adnate to wing, 1.4–2.4 mm tall, 1.0–2.9 mm long; long axis of seed perpendicular to medial edge of wing; medial side of wing may have slight concavity proximal to seed body; admedial side of wing convex; seed body on proximal end; admedial edge curves convexly around to distal end forming a diagonal edge 8.0–9.4 mm long; wing striations parallel to medial edge and slightly undulatory and different widths; widest part of wing proximal to middle half.

Remarks. The fossil conforms to Wolfe and Schorn's (1990) "atypical *Pinus* 1" having an adnate seed body, small admedial wing (< 1 cm) and seed body (< 3 mm). This seed differs from *Pinus* sp. S4 by having the proximal and middle portion of the wing being the widest and being wider.

***Pinus* sp. S6**

Text-fig. 3t

Material. USNM PAL 619965, 622044, 622339, 623123, 776561.

Localities. Disbrow Creek and Park.

Description. Winged seed linear, at least 12.9–21.4 mm long, 3.9–6.4 mm wide; seed body circular on proximal edge 1.8–2.1 mm wide; abmedial side of wing gradually or abruptly widens partly along seed body; striations undulatory and different widths.

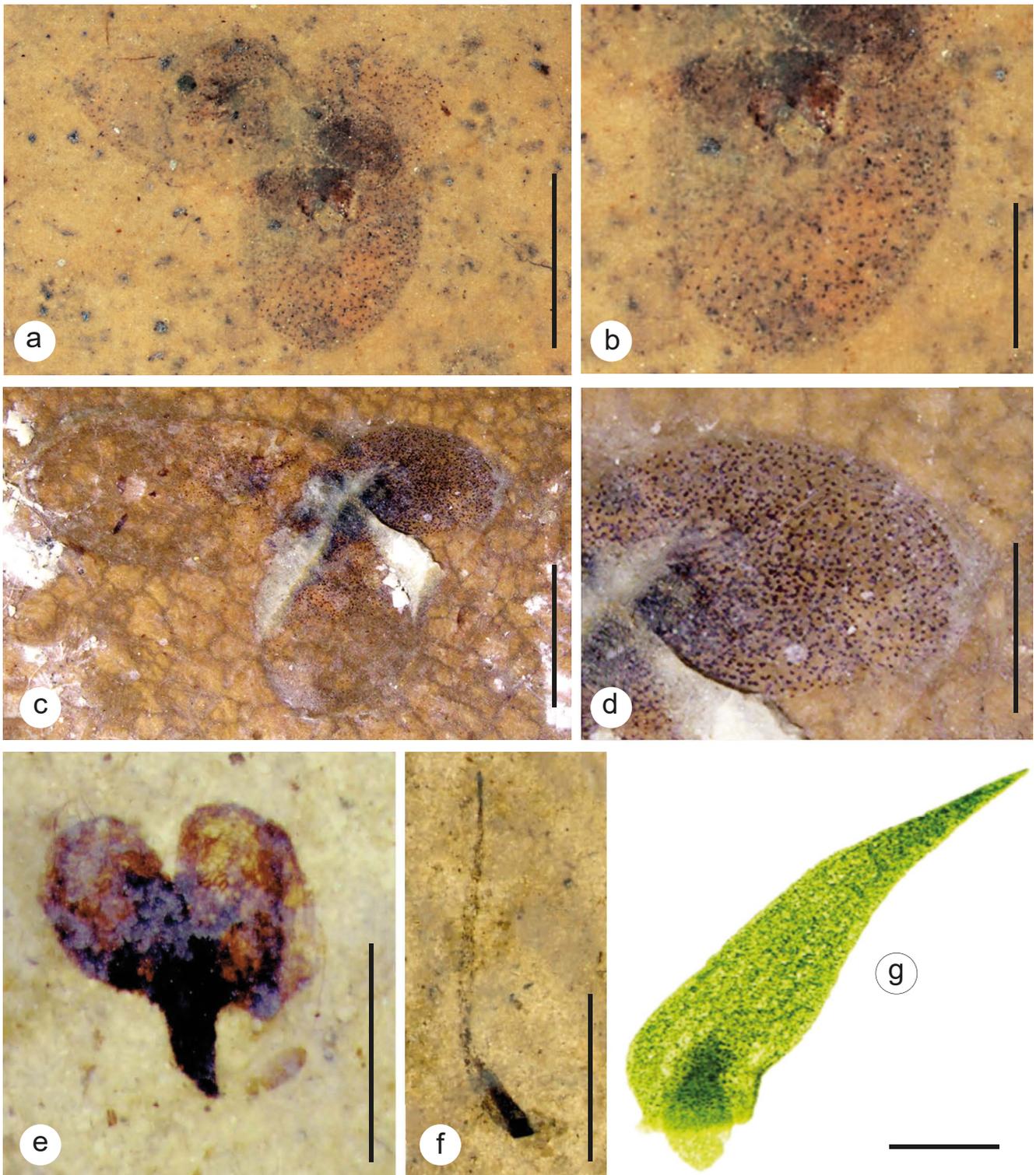
Remarks. *Pinus* subg. *Pinus* has seed bodies that are adnate to the wing and do not disarticulate (Wolfe and Schorn 1990). This pine has an adnate wing, admedial edge longer than one cm and seed body smaller than 3 mm conforms to Wolfe and Schorn's (1990) atypical *Pinus* 3 group.

Comments on *Pinus*

The Kishenehn pine seeds are summarized in Tab. 2. Pines are common and widespread amongst western North American Eocene and Oligocene localities. Erwin and Schorn (2005) recognized both hard and soft pines from the mid-Eocene Thunder Mountain flora of Idaho from Axelrod's (1998) initial material: *Pinus* cf. *crossii* AXELROD (fascicle, *Pinus* subg. *Strobus*), *Pinus* cf. *sanjuanensis* AXELROD (fascicle, *Pinus* subg. *Strobus*) and *Pinus* cf. *baileyi* AXELROD (ovulate cone, *Pinus* subg. *Pinus*). Ecologically, *Pinus* subg. *Pinus* tends to be more fire-adapted than *Pinus* subg. *Strobus* which is more tolerant to precipitation and temperature stresses (Singh et al. 2021). Thus, either the Kishenehn Basin experienced both fire and drought and/or severe cold temperatures or the basin is picking up a regional signature with *Pinus* subsp. *Strobus* coming in from the highlands. Incidentally, *Pinus* sp. Seed 6 likely would have been the more efficient disperser due to its small seed body and large wing (Singh et al. 2021). Seeds weighing less than 90 mg are likely to be dispersed by the wind rather than animals, although secondary dispersal by animals may occur even in wind-dispersed pines (Van der Wall 1992, Benkman 1995). It is also difficult to say if all six pine seed morphotypes represent six truly distinct species because pines often hybridize (Critchfield 1975) and seed shape and size can vary depending on the part of the cone it developed in (Erwin and Schorn 2005).

Summary of the conifers

Here, we recognize leaves and possible miniature seeds of *Metasequoia*; a *Juniperus* leafy twig; four morphospecies of cupressaceous foliage that differ in leaf size, apex shape, leaf overlap patterns and branching patterns; one *Abies* seed; one *Larix* seed and a likely *Larix* cone; two species of *Picea* seeds; a Pinaceae leaf that cannot be assigned to genus; three Pinaceae cones that cannot be assigned to genera; a *Pinus* cone that cannot be identified to the subgenus level; a *Pinus* subg. *Strobus* cone; three species of *Pinus* subgenus *Strobus* seeds; a cone scale from *Pinus* subg. *Pinus* and three species of *Pinus* subg. *Pinus* seeds. The Dewey Mine florule of the



Text-fig. 4. Lemnoideae from the Kishenehn Formation. a: USNM PAL 625611 *Spirodela* sp. showing fronds, prophyllum and daughter plant with brown pigment cells. Scale bar 2 mm. b: Close up of USNM PAL 625611 prophyllum and brown pigment cells. Scale bar 1 mm. c: USNM PAL 768304 *Spirodela* sp. showing fronds, prophyllum and daughter plant with brown pigment cells. Scale bar 2.5 mm. d: Close up of USNM PAL 768304 daughter plant with brown pigment cells. Scale bar 2.5 mm. e: USNM PAL 620300 *Lemna* sp. showing fronds with aerenchyma and pseudoroot. Scale bar 1 mm. f: USNM PAL 626140 *Wolffia* sp. “tongue-shaped” multicellular frond with brood pouch at the base. Scale bar 2 mm. g: Modern *Wolffia caudata* frond with brood pouch and daughter plant from Pagliuso et al. 2018. Scale bar 1 mm.

mid-Eocene Thunder Mountain flora of Idaho, in comparison to the Kishenehn, represents a coniferous forest, unusual for its time considering most paleofloras of mid-Eocene age are broadleaf or mixed (Axelrod 1998). The Kishenehn shares Cupressoidae foliage, *Abies*, *Larix*, *Picea* and *Pinus* (both

Pinus subg. *Strobus* and *Pinus* subg. *Pinus*) with the Thunder Mountain flora but lacks cf. *Tsuga* and cf. *Sequoia* (Erwin and Schorn 2005). The Kishenehn also has *Metasequoia* and *Juniperus* and contains a larger diversity in Cupressoidae foliage, which is not present in the Thunder Mountain flora.

The presence of *Metasequoia* in the Kishenehn flora may be due to the fact that there was a paleolake at Kishenehn or that the Thunder Mountain flora, estimated to have been between 1,730 and 3,163 m by Axelrod (1998), may have been higher than *Metasequoia*'s elevational tolerance (Silba 1986).

Division Angiospermae LINDLEY

Family Araceae JUSS.

Genus *Spirodela* SCHLEID.

Text-fig. 4a–d

Material. USNM PAL 624518, 625611, 768304.

Localities. Dakin and Spring.

Description. Plants with elliptical fronds 1.1–3.9 mm long, 1.5–2.5 mm wide; prophylla present, 0.8–1.1 mm long, 1.1–1.4 mm wide; brown pigment cells present.

The presence of large prophylla and brown pigment cells places these plants within *Spirodela* (Armstrong 2021). Prophylla are absent in *Lemna* L. and reduced in *Landoltia* LES et D.J.CRAWFORD (Armstrong 2021). We interpret the brown, circular dots that are concentrated near the prophylla and more dispersed in the distal portion of the leaves as brown pigment cells. Brown pigment cells are absent in *Lemna* but present in *Spirodela* (Armstrong 2021). *Spirodela* was described from the Paleocene of Alberta and Saskatchewan (Dawson 1875, Berry 1935, McIver and Basinger 1993) and the middle Eocene of Wyoming (MacGinitie 1974), but these fossils were subsequently transferred to the extinct araceous genus *Limnobiophyllum* KRASSILOV (Kvaček 1995, Stockey et al. 1997).

Genus *Lemna* L.

Text-fig. 4e

Material. USNM PAL 620300.

Locality. Park.

Description. Leaves 0.9 mm long, 0.5–0.6 mm wide; elliptical; aerenchyma present; pseudoroot 0.4 mm long, 0.2 mm wide with slanted terminus.

Remarks. The small size, elliptical leaves, presence of a pseudoroot and lack of venation are characters of the aquatic araceous subfamily, Lemnoideae. The lack of brown pigment cells, which we might expect to preserve in these cellularly preserved compressions (and which do preserve in the *Spirodela* fossils), rules out its placement in *Spirodela* or *Landoltia* and the broad elliptical shape of the fronds contrasts with the more narrow ellipses of *Wolffia* HORTEL ex SCHLEID and the narrow fronds of *Wolffiella* (Armstrong 2021). Note the name of the distinctive surficial cells is brown pigment cells. While they are brown in modern plants we would not necessarily be able to determine the color in the fossils. Thus, the leaf shape and lack of brown pigment cells support the placement of this specimen in *Lemna*. In North America, *Lemna* fossils are known from the Miocene of Mississippi (McNair et al. 2019). The Kishenehn fossils are the oldest record of *Lemna*, predating Oligocene occurrences in Eurasia (Dorofeev 1963). Another notable occurrence of Cenozoic Lemnoideae is that of the *Limnobiophyllum* leaf and root fossils from the Late Cretaceous through Oligocene

of western North America (Hoffman 1995, Kvaček 1995, McIver and Basinger 1993, Stockey et al. 1997). *Limnobiophyllum* differs from our fossils by having veined leaves, branching roots and size (leaves are 1–2 cm wide) (Kvaček 1995, Stockey et al. 1997).

Genus *Wolffiella* HEGELM.

Text-fig. 4f

Material. USNM PAL 622956, 626140.

Localities. Deep Ford and Disbrow Creek.

Description. Frond triangular, 4.4–4.7 mm long, 0.3–0.7 mm wide at base, base flat to curved, budding pouch triangular, 0.9–1.2 mm tall, 0.3–0.7 mm wide, aerenchyma present.

Remarks. The slender triangular fronds with aerenchyma and budding pouches are diagnostic of *Wolffiella* (Armstrong 2021). This specimen is not the dispersal hair of a *Typha* fruit because it is a multicellular frond. *Wolffiella* plants can exhibit a variety of morphologies including ovate, “tongue” and sickle shaped (Acosta et al. 2021) (Text-fig. 4g). The size range of these specimens also fits the size range of modern North American *Wolffiella* fronds (4.4–4.7 mm for the fossils, 1–9 mm for the modern) (Landolt 2020). Ours would fit in the “tongue” category, which does not occur in the other genera of Lemnoideae. These are the first reported *Wolffiella* fossils. Today there are 10 species of this floating aquatic plant across the Americas and Africa (Landolt 2020). Species in the US are concentrated in the Southwest and Southeast (Landolt 2020).

Family Potamogetonaceae RCHB.

Genus *Potamogeton* L.

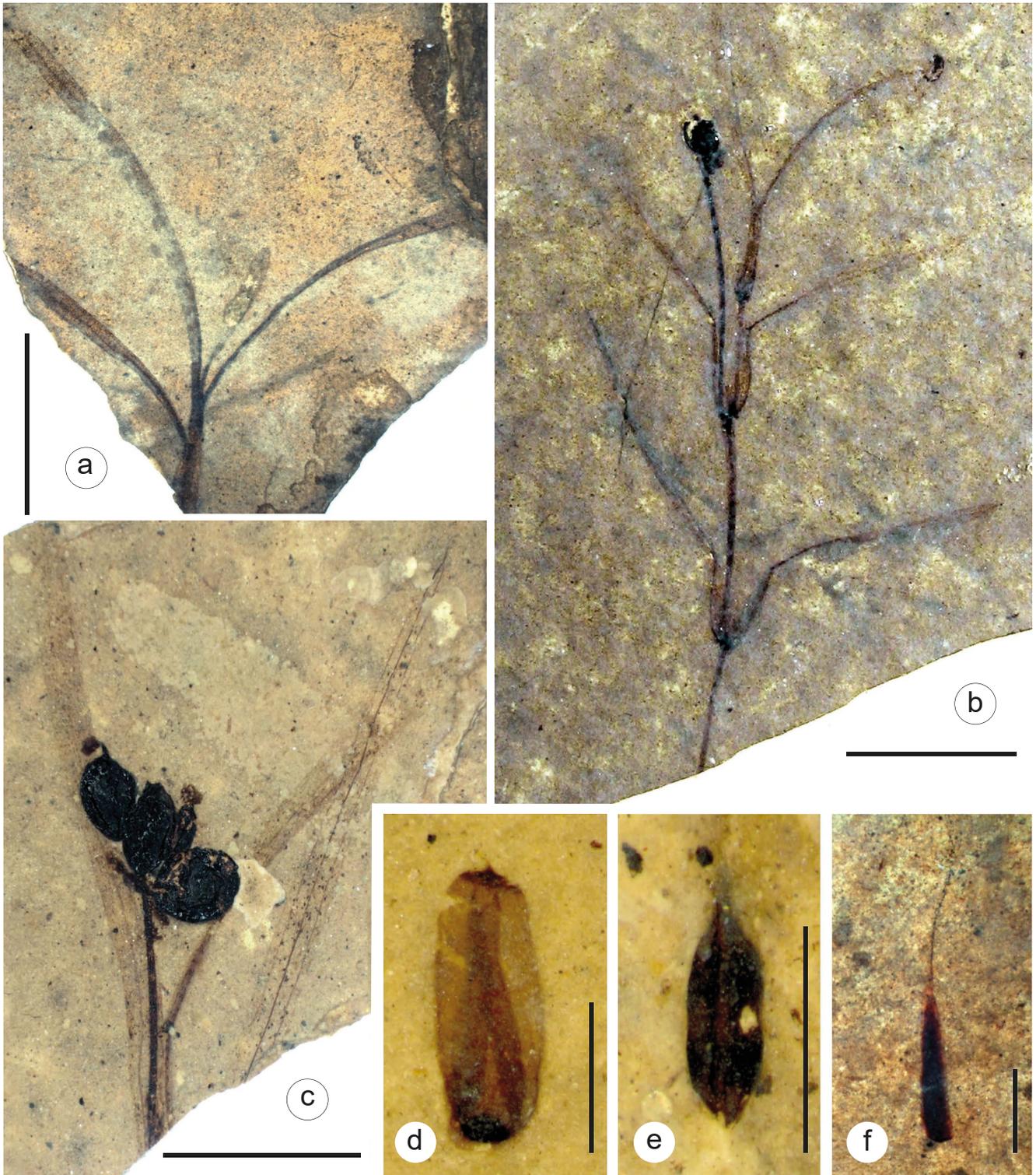
Text-fig. 5a–c

Localities. Deep Ford, Disbrow Creek, Park and Spring.

Material. USNM PAL 622670, 622675, 623125, 626043, 625757, DMNH EPI.48225, 48188.

Description. Stem 0.2–0.7 mm wide; leaves opposite; nodes thick; leaves at least 24.9 mm long, 1.2–1.4 mm wide; 2° 1° 2° (where left to right the veins are thin, thick then thin, see fig. 1a, b in Robil et al. (2021) for comparison) parallel venation type with veins joining to the center vein near leaf apex; apex rounded; margin entire; pigment or glandular cells present; fruits flat, circular drupes, 2.24–3.10 mm tall, 1.8–2.6 mm wide, 0.6 mm thick; style pointed with persistent stigmatic region; pedicel 0.1 mm long and 0.1 mm wide; four fruits on a raceme with peduncle 9 mm long and 0.2 mm wide.

Remarks. The aquatic genus, *Potamogeton*, is identifiable from leafy stems bearing infructescences. The genus is distinguished by its opposite narrow leaves, and circular, flat fruits with a pointed apex and persistent styles that are borne in racemes (Manchester 2001). Fruits and leaves of *Potamogeton* have also been recognized from the late Eocene Florissant Formation of Colorado (Manchester 2001) and leaves from the mid-Eocene Thunder Mountain flora of Idaho (Axelrod 1998).



Text-fig. 5. *Potamogeton* sp. and *Typha* sp. from the Kishenehn Formation. a: USNM PAL 622670 *Potamogeton* sp. stem and leaves. Scale bar 1 cm. b: DMNH EPI. 48225 *Potamogeton* sp. showing vegetative structures and fruit. Scale bar 1 cm. c: USNM PAL 623125 *Potamogeton* sp. infructescence with leaves. Scale bar 5 mm. d: USNM PAL 622997 follicle body of *Typha* sp. showing longitudinal opening and apical tuft/stylar remnant. Scale bar 1 mm. e: USNM PAL 623087 follicle body of *Typha* sp. showing longitudinal opening. Scale bar 1 mm. f: USNM PAL 621989 *Typha* sp. carpodium. Scale bar 2 mm.

Family Typhaceae Juss.

Genus *Typha* L.

Text-fig. 5d–f

Material. USNM PAL 729860, 621989, 622997, 623087, 623129, 623144, 717449, 625390, 625721.

Localities. Dakin, Disbrow Creek, Park and Spring.

Description. Carpodium 2.5–6.8 mm long, 0.6–0.9 mm wide; carpodium body obovate with rounded apex, 0.6–3.5 mm long, 0.6–0.9 mm wide tapering to gynophore; gynophore 1.9–3.6 mm long, vein sometimes visible

going into carpodium from gynophore; follicle cylindrical fusiform, 1.9–2.1 mm long, 0.7–0.8 mm wide; coat thin; edges straight; one pole with small tuft (remnant style) 0.1 mm long, or rounded poles; lateral edges flat; sulcus running between poles; fruit body elongated ellipse, 1.1–2.1 mm long, 0.3–0.7 mm wide; cylindrical projections at pole(s) gently tapering distally 0.1–0.3 mm tall, 0.1–0.2 mm wide proximally, 0.1 mm distally; single longitudinal groove; psilate sculpture.

Remarks. Although the fossils are similar in shape and size to *Wolffiella* there is a stipe and vein in the developing *Typha* fruit that is not present in *Wolffiella*. The thin wall of the follicle can be observed in modern cattails (Iowa Plants 2012).

This fossil bears some resemblance in shape and size to fruits of modern *Elodea* MICHX. (Hydrocharitaceae), a genus found throughout the Americas today (Kirkbride et al. 2000, Haynes 2020). *Hydrilla* RICH. is similar in morphology but is smaller (less than 1 mm) and is more sculptured with longitudinal grooves (Kirkbride et al. 2000). Similarly shaped seeds can also be found in *Plantago* L. (Plantaginaceae), which is globally distributed (except in Antarctica) (Canadian Food Inspection Agency 2017) and in *Carex* sp. (Bhandari et al. 2010, 2011). Despite similarities with *Elodea*, *Hydrilla* and *Plantago*, the fossil fruits have polar extensions that the aforementioned plants do not have. The lateral edges of *Elodea* (Kirkbride et al. 2000, Haynes 2020) and *Carex* L. fruits are more rounded rather than flat, as observed (Bhandari et al. 2010, 2011). *Carex* scales can be triangular but lack the polar extension and possess foliar lateral extensions near the base, which do not appear in the fossil (Minnesota Wildflowers 2023a).

Typha has been identified based on pollen from the Paleocene Fort Union Formation of Montana (Wilson and Webster 1946). Macrofossils of *Typha* and/or *Sparganium* are reported from the early Eocene Green River Formation of Wyoming (Grande 1984), the Eocene Hat Creek Formation and Ootsa Lake Group of British Columbia (Blackburn 1982, Ludvigsen 2001), the middle Eocene Thunder Mountain flora of Idaho (Axelrod 1998) and the John Day Formation of Oregon (Manchester 2000). Both pollen and fruits have been recovered from exposures of the Kishenehn in Canada (Hopkins and Sweet 1976).

Family Ceratophyllaceae GRAY

Genus cf. *Ceratophyllum* L.

Text-fig. 6a

Material. USNM PAL 625188.

Locality. Spring.

Description. Fruit elliptical, 2.9 mm long (body 2.6 mm long), 1.5 mm wide; basal spine 0.3 mm long, 0.2 mm wide; three short visible lateral spines on the antipodal side 0.1 mm long; small indentations on the surface.

Remarks. We interpret this as an eroded specimen retaining only remnants of the original spines. By inference from symmetry, a total of at least six short lateral spines can be inferred. *Ceratophyllum muricatum* CHAM. subsp. *incertum* (BERRY) HERENDEEN, LES et DILCHER is known from

the early and mid-Eocene of the Green River Formation of Wyoming and the Claiborne Formation of Tennessee (Herendeen et al. 1990). However, *C. muricatum* subsp. *inertum* is larger (2.8–4.0 mm long and 2.0–2.3 mm wide) and has more lateral spines (8–11) (Herendeen et al. 1990).

Family Ranunculaceae JUSS.

Genus cf. *Thalictrum* L.

Text-fig. 6b

Material. USNM PAL 722388.

Locality. Dakin.

Description. Follicle 2.6 mm long, 1.4 mm wide at the widest; bulbous with one end tapering to a point and the antipodal side ending with a small cylinder measuring 0.4 mm tall and 0.5 mm wide; seven parallel striations 0.1 mm wide extend longitudinally.

Remarks. Longitudinal ribbing along a chimney lamp-shaped follicle is characteristic of *Thalictrum*. Fossil *Thalictrum* fruits are known from the Oligocene and Miocene of Europe (Szafer 1961, Dorofeev 1963, Mai 1995) and the Pleistocene of Nepal (Bhandari et al. 2009, 2010, 2011). If confirmed, this would be the oldest *Thalictrum* ca. 20 Ma older than estimates for crown of that genus (Soza et al. 2013).

Family Platanaceae T. LESTIB.

Genus *Platanus* L.

Text-fig. 6c–f

Material. USNM PAL 622299, 768140.

Localities. Dakin and Disbrow Creek.

Description. Achene obovate 8.8–8.9 mm long, 1.7 mm wide with flat base rounding to acute apex and elongate style 3.7–4.1 mm long and 0.2 mm wide, single seed obovate to fusiform preserved inside 3.3–5.1 mm long and 0.4–0.9 mm wide with thickened micropylar end, many dispersal hairs 0.5–1.8 mm long arise from base of achene directed apically.

Remarks. The presence of dispersal hairs distinguishes *Platanus* fruits from the fruit of *Macginicarpa* (the fossil genus used for fruits associated with *Macginitiea* J.A. WOLFE et W. WEHR in Manchester leaves) (Manchester 1986, Huegele and Manchester 2022). *Platanus* fruits are known from the mid-Eocene Clarno Nut Beds of (Manchester 1994). *Platanus* is an indicator for riparian environments (Nixon and Poole 2003).

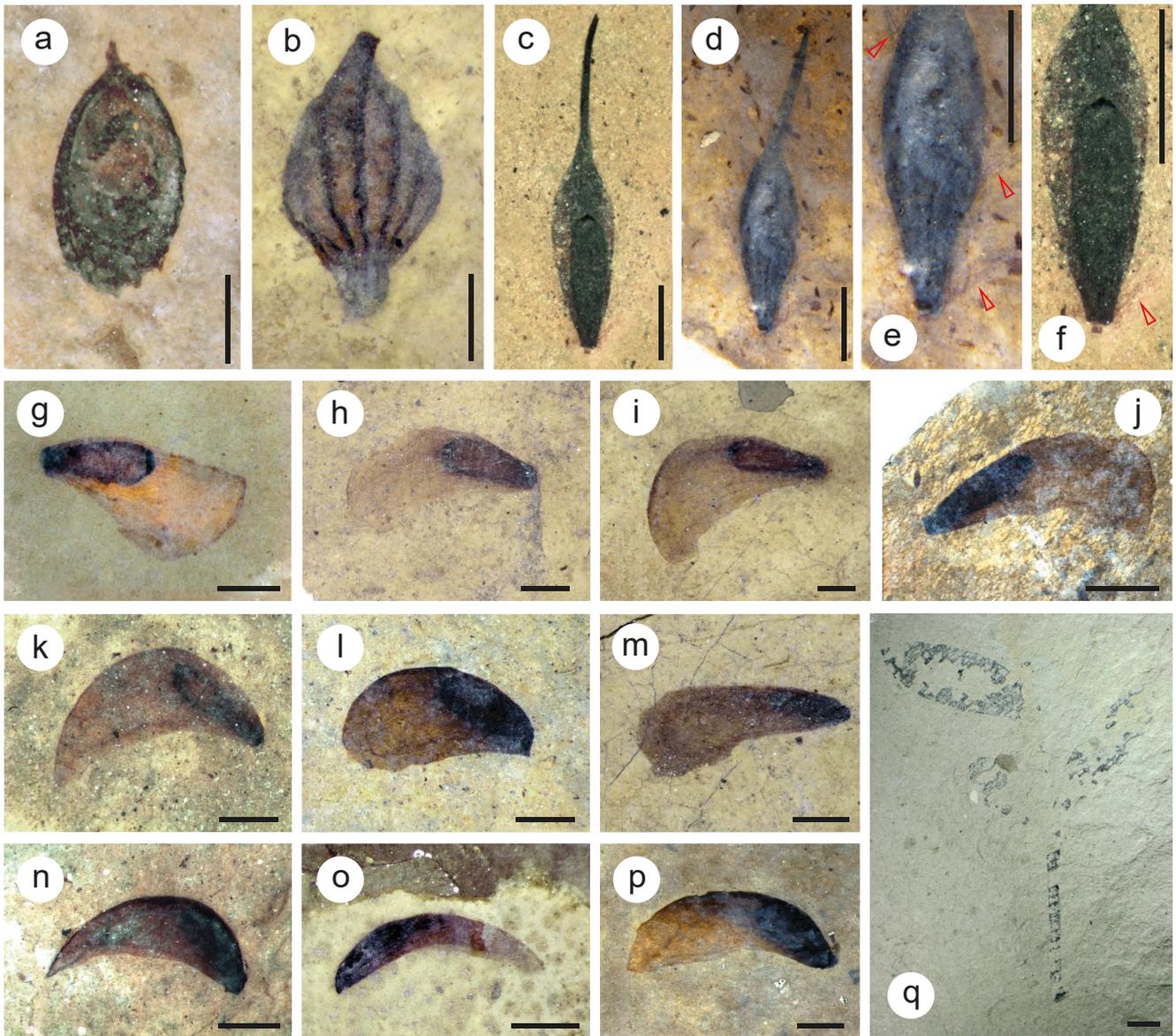
Family Cercidiphyllaceae ENGL.

Genus *Carpolithes* BRONGN.

***Carpolithes lunatus* HICKEY**

Text-fig. 6g–p

Material. USNM PAL 621411, 622713, 622294, 623312, 624006, 624179, 624447, 624499, 624509, 624556, 624648, 624684, 624710, 624778, 717434, 717553, 712990, 625251, 625257, 625269, 625286, 625358, 625406, 625485, 625500, 625541, 625560, 625572, 625609, 625618, 625647, 625651, 625661, 625662, 625676, 625752, 625764, 625776, 625783.



Text-fig. 6. a: USNM PAL 625188 cf. *Ceratophyllum* fruit. Scale bar 1 mm. b: USNM PAL 722388 cf. *Thalictrum* sp. Scale bar 2 mm. c: USNM PAL 622299 *Platanus* sp. achene with prominent seed body. Scale bar 2 mm. d: USNM PAL 768140 *Platanus* sp. achene with dispersal hairs. Scale bar 2 mm. e: Close-up of USNM PAL 768140 *Platanus* sp. achene with red arrows pointing to dispersal hairs. Scale bar 2 mm. f: USNM PAL 622299 *Platanus* sp. achene with red arrows pointing to hairs. Scale bar 2 mm. g: USNM PAL 623312 winged seed of *Carpolithes lunatus*. Scale bar 1 mm. h: USNM PAL 625269 winged seed of *Carpolithes lunatus*. Scale bar 1 mm. i: USNM PAL 625257 winged seed of *Carpolithes lunatus* with highly curved wing. Scale bar 1 mm. j: USNM PAL 624499 winged seed of *Carpolithes lunatus*. Scale bar 1 mm. k: USNM PAL 622294 winged seed of *Carpolithes lunatus* with raphe wrapping along wing towards the chalazal end of the seed body. Scale bar 1 mm. l: USNM PAL 717434 winged seed of *Carpolithes lunatus* with raphe wrapping along wing towards the chalazal end of the seed body. Scale bar 1 mm. m: USNM PAL 625251 winged seed of *Carpolithes lunatus* with raphe wrapping along wing towards the chalazal end of the seed body. Scale bar 1 mm. n: USNM PAL 625541 elongated winged seed of *Carpolithes lunatus* with raphe wrapping along wing towards the chalazal end of the seed body. Scale bar 1 mm. o: USNM PAL 625286 elongated winged seed of *Carpolithes lunatus*. Scale bar 1 mm. p: USNM PAL 624179 winged seed of *Carpolithes lunatus* with raphe wrapping along wing towards the chalazal end of the seed body. Scale bar 1 mm. q: USNM PAL 620034 cf. *Jenkindsella knowltonii*. Scale bar 2 mm.

Localities. Dakin, Disbrow Creek, Park and Spring.

Description. Winged seeds with seed body on one side; full seeds ranging from 2.5–5.5 mm long and 0.5–4.00 mm wide; seed bodies obovate to semi-fusiform, 1.1–3.3 mm long and 0.3–1.5 mm wide; seed body oblique with proximal end tilting to the ventral side of the wing and distal side tilting to the dorsal side of the wing; seed wings straight or curved with distal end straight or curved proximally; wing finely striate; raphe wrapping around the margin of the

wing or turning dorsally near the middle to continue along the margin to the chalazal end of the seed body.

Remarks. Seeds with this morphology match the morphospecies *Carpolithes lunatus* HICKEY. Such seeds co-occur with or are a constituent of the fruits known as *Jenkindsella* REID et CHANDLER, *Joffrea* CRANE et STOCKEY, *Nyssidium* HEER and are commonly associated with the leaves known as *Trochodendroides* BERRY (Crane and Stockey 1985, 1986, Golovneva and Alekseev 2017). Further

investigations are needed to differentiate these plants based on seeds (Golovneva and Alekseev 2017). Brown (1939) documented cercidiphyllaceous elements from 30 localities in the western US and Dakotas from Cretaceous through Oligocene.

Genus *Jenkinsella* E.REID et M.CHANDLER
cf. *Jenkinsella knowltonii* GOLOVNEVA et P.I.ALEXEEV
Text-fig. 6q

Material. USNM PAL 620034.

Locality. Park.

Description. Raceme 23.4 mm long with three widely spaced follicles; peduncle 0.8 mm wide; follicles elliptical with truncated base and acute apex, 10.2–11.0 mm long, 3.2–4.0 mm wide.

Remarks. Infructescences of *Jenkinsella knowltonii* are generally 35–50 mm long, have 5–7 widely spaced follicles that are 10–16 mm long and 4–7 mm wide (Golovneva and Alekseev 2017). The Kishenehn specimen is slightly shorter, is lacking the preservation of reproductive shoots and has fewer follicles though this could be a preservational issue. *J. knowltonii* is known from the Paleocene Denver Formation of Colorado (Golovneva and Alexeev 2017).

Family Haloragaceae R.BR.
Genus cf. *Myriophyllum* L.
Text-fig. 7a

Material. USNM PAL 722490.

Locality. Dakin.

Description. Endocarp elliptical 2.1 mm long, 1.1 mm wide; four to five lateral projections on each side measuring 0.2–0.4 mm long and 0.1–0.3 mm wide at the base.

Remarks. *Myriophyllum* fruits are rectangular to elliptical and have short, lateral projections. Pleistocene leaf fossils are known from Kashmir (Puri 1951) and endocarps from Nepal (Bhandari et al. 2009, 2010, 2011). Another fossil occurrence attributed to Haloragaceae is *Tarahumara sophiae* HERN.-CASTILLO et CEV.-FERRIZ from the Campanian-Maastrichtian of northern Mexico (Hernandez-Castillo and Cevallos-Ferriz 1999). The Kishenehn specimen may be the oldest macrofossil of the genus.

Family Salicaceae MIRB.
Genus *Populus* L.
***Populus* sp.**
Text-fig. 7b

Material. USNM PAL 624027.

Locality. Dakin.

Description. Capsule 4.1 mm long, 2.8 mm wide; pedicel 5.1 mm long, 0.4 mm wide; pedicel thick at apex and base and thinner in center with a thickened scar of five detached sepals at junction with base of the fruit; three-valved ovate loculicidal capsule; apices of capsule valves slightly rounded.

Remarks. Fruits of *Populus wilmattae* COCKERELL, *P. tidwellii* MANCHESTER, JUDD et HANDLEY and those associated with *P. cinnamomoides* (LESQ.) MACGINITIE have been described from the Green River Formation (Manchester et al. 1986, Manchester et al. 2006). Although the capsule from Kishenehn is the same in shape, valve number, dehiscence type, it is about half the size as those of *P. tidwellii* and *P. cinnamomoides* from the Green River Formation (Manchester et al. 2006), but they conform in size with those of *P. wilmattae* (3–4.5 mm wide and 5 to 7 mm long; Manchester et al. 1986). Fruits of *Pseudosalix handleyi* L. BOUCHER, MANCHESTER et JUDD, from the Green River Formation, are somewhat larger (5.5–7.5 mm long and 3.0–4.5 mm wide), but are similar in shape, valve number and dehiscence type. *P. handleyi* possesses longitudinal ribs which are absent in the Kishenehn fossil and thus the Kishenehn fossil cannot be placed in that genus (Boucher et al. 2003). Leaves attributed to *Populus* have been recognized from the mid-Eocene Thunder Mountain flora of Idaho (Axelrod 1998). Although *Populus* was a dominating element of the Green River flora of Colorado and Utah, only a single fruit is known from the Kishenehn collections.

Family ?Polygalaceae HOFFMANNS. et LINK
Genus *Deviacer* MANCHESTER
***Deviacer wolfei* MANCHESTER**
Text-fig. 7c

Material. USNM PAL 717328.

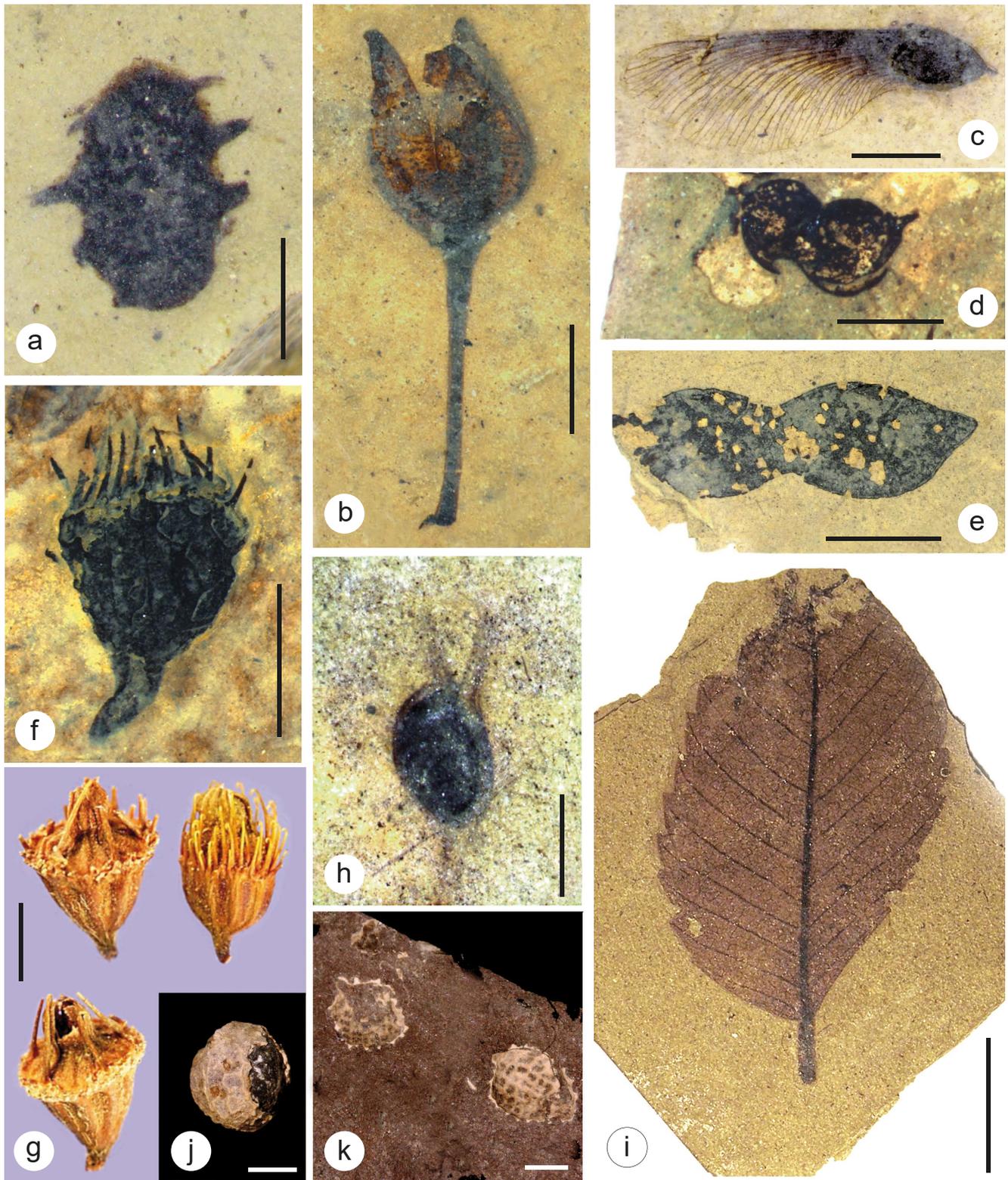
Locality. Disbrow Creek.

Description. Samara 2.1 cm long, 0.7 cm wide at widest point of wing; nutlet elliptical 0.5 cm long and 0.3 cm wide; peduncle persistent, small projection pointing distally along the dorsal side of the wing near the apex of the nutlet; dorsal side of wing slightly convex; ventral side of wing becomes wider just past the nutlet apex and reaches full width $\frac{2}{3}$ of the way to the distal end; veins originate near the nutlet apex and curve down to the ventral side of the wing, generally dichotomizing, occasionally anastomosing and cross veins with proximal veins more likely to anastomose.

Remarks. Fruits of *Deviacer wolfei* are known from the similarly aged Nut Beds of the Clarno Formation of central Oregon; they are samaras with elliptical nutlets, persistent styles, dorsal projections and fall within the same size range and ratios (Manchester 1994, Chen and Manchester 2015). *Deviacer* fruits that appear similar but are unassigned to a species are also known from the early Eocene Republic flora of eastern Washington (Pigg et al. 2008) and early Eocene Falkland flora of British Columbia (Smith et al. 2012). Late Paleocene fossil fruits with this morphology from Almont, North Dakota with anatomical preservation were named *Paleosecuridaca* PIGG, DEVORE et M.F. WOJC. (Pigg et al. 2008). According to those authors, similarities suggest that at least some of these fruits are assignable to Polygalaceae.

Family Fabaceae LINDL.
Fabaceae sp. 1
Text-fig. 7d

Material. USNM PAL 621987.



Text-fig. 7. a: USNM PAL 722490 cf. *Myriophyllum* fruit. Scale bar 1 mm. b: USNM PAL 624027 three-valved *Populus* sp. capsule on pedicel. Scale bar 3 mm. c: USNM PAL 717328 *Deviacer wolfei* samara. Scale bar 5 mm. d: USNM PAL 621987 Fabaceae sp. 1 Legume fruit showing persistent style. Scale bar 2 mm. e: USNM PAL 625803 Fabaceae sp. 2 fruit. Scale bar 5 mm. f: USNM PAL 620816 *Agrimonia* sp. fruit. Scale bar 3 mm. g: Modern *Agrimonia pubescens* fruit (image by Tracey Slotta, United States Department of Agriculture National Resource Conservation Service Plants Database). h: USNM PAL 621976 *Ulmus* sp. F1 fruit showing two persistent styles. Scale bar 2 mm. i: DMNH EPI.48205 *Ulmus* sp. L1 leaf. Scale bar 1 cm. j: UF 19652-86483 endocarp of *Celtis* sp. k: UF 19652-86484 Endocarps of *Celtis* sp.

Locality. Disbrow Creek.

Description. Legumes containing two circular seeds; fruit 3.5 mm long, 1.9 mm wide; fruit constricted

between adjacent seeds such that width decreases to 1.2 mm between seeds; seeds 1.4–1.5 mm wide; style persistent and triangular 0.4 mm long and 0.2 mm wide at base.

Fabaceae sp. 2

Text-fig. 7e

Material. USNM PAL 625803.

Locality. Spring.

Description. Legume containing at least two circular seeds; fruit at least 15.9 mm long, 5.0 mm wide, constricted to 2.9 mm wide between seeds; seeds 5.7–5.8 mm wide; legume apex triangular 1.7 mm wide at base; 1.1 mm long, sutural wing 0.3 mm wide.

Comments on Fabaceae

The fruit of Fabaceae sp. 2 can be differentiated from Fabaceae sp. 1 by its larger size and somewhat stronger constriction around the seeds.

Family Rosaceae JUSS.

Genus *Agrimonia* L.

***Agrimonia* sp.**

Text-fig. 7f

Material. USNM PAL 620816, 621198.

Locality. Park.

Description. Pedicel 1.7 mm long, 0.4 mm wide at base and 0.9 mm wide at apex; achene 2.6–4.2 mm long, 1.6–3.8 mm wide; at least 7–16 apically extend linear bristles arising from apical portion of fruit; bristles 1.0–1.8 mm long, 0.1–0.3 mm wide, apices acute or tapering distally with rounded apices, two filaments on USNM PAL 621198 0.6 mm long, 0.04 mm wide.

Remarks. This fossil corresponds in size and morphology to fruits of *Agrimonia* with a wide calyx, wide-ribbing on the calyx and many persistent bristles (Guo 1998). Whereas in some *Agrimonia* species the bristles are hooked in the fruit, they can be erect in others (Kline and Sørensen 2020: fig. 7g). We also compared this fossil to petalless inflorescences of asteraceous taxa like *Bidens* L., *Rhodanthemum* B.H. WILCOX, K. BREMER et HUMPHRIES, and *Leucanthemum* SAMP. but those genera have individual bracts that surround the base of the inflorescence rather than an achene topped with bristles (pers. obs.). The Kishenehn specimen represents the first fossil record of the genus.

Family Ulmaceae MIRB.

Genus *Ulmus* L.

***Ulmus* sp. F1**

Text-fig. 7h

Material. USNM PAL 621976.

Locality. Disbrow Creek.

Description. Fruit a samara, length 4.3 mm, width 1.9 mm, fruit body excluding stipe and styles 2.8 mm long, wing narrowing (0.3 mm) surrounding central seed body, seed body elliptical 2.1 mm long and 1.3 mm wide, two rectangular, prominent styles 1.2 mm long and 0.7 mm wide emerging apically in a V-shaped configuration.

Remarks. This fruit bears a resemblance to those of *Ulmus okanaganensis* DENK et DILLHOFF from the early

Eocene of British Columbia and Washington (Denk and Dillhoff 2005). However, *U. okanaganensis* lacks a visible wing and has styles that are more tapered and curved to the center (Denk and Dillhoff 2005). There is also a similarity to fruits named as *Ulmus* sp. from the same time and area as *U. okanaganensis* (Denk and Dillhoff 2005), but the styles differ from this being more tapered and proximally curved.

***Ulmus* sp. L1**

Text-fig. 7i

Material. DMNH EPI.48205.

Locality. Disbrow Creek.

Description. Leaf elliptical, 4.4 cm long, 2.0 cm wide; petiole 0.4 cm long, 0.1 cm wide; base asymmetrical, apex not preserved; venation pinnate, secondaries craspedodromous, excurrent and arising at 41°, curving apically near the margin into the apex of the tooth, secondary pair spaced every ca. 2.7 mm apart; intersecondary veins present; teeth one order, regularly spaced, proximal flank convex and distal flank straight or concave.

Remarks. This leaf can be placed confidently in the Ulmaceae because of its asymmetrical lamina, short, stout petiole, pinnate venation and marginal teeth with submedial enervation. Leaves with one tooth per secondary vein occur in *Zelkova*, *Hemiptelea*, *Cedrelospermum*, and occasionally *Ulmus*. Although most species of *Ulmus* have compound teeth with multiple teeth per secondary vein, simple teeth, organized one per secondary vein, occur in some species of *Ulmus*, as confirmed for *Ulmus okanaganensis* (where such leaves are attached to twigs bearing the diagnostic fruits). We infer that this leaf represents *Ulmus*, by its association with the fruit described above.

Family Cannabaceae MARTINOV

Genus *Celtis* L.

Text-fig. 7j, k

Material. UF 19652-86483, 19652-86484, 19652-86485, 19652-86486, 19652-86487, 19652-86488.

Locality. M3.

Description. Endocarp calcareous, ovoid, 4.7 mm long, 3.5 mm wide, with reticulate surface ridging, areoles of the reticulum square; endocarp 7 squares wide and about 8 squares tall.

Remarks. A calcified endocarp with reticulate sculpture enables us to place this fossil in *Celtis*. Such endocarps are commonly known from Eocene deposits (Manchester 1989, 1994).

Family Juglandaceae DC. ex PERLEB

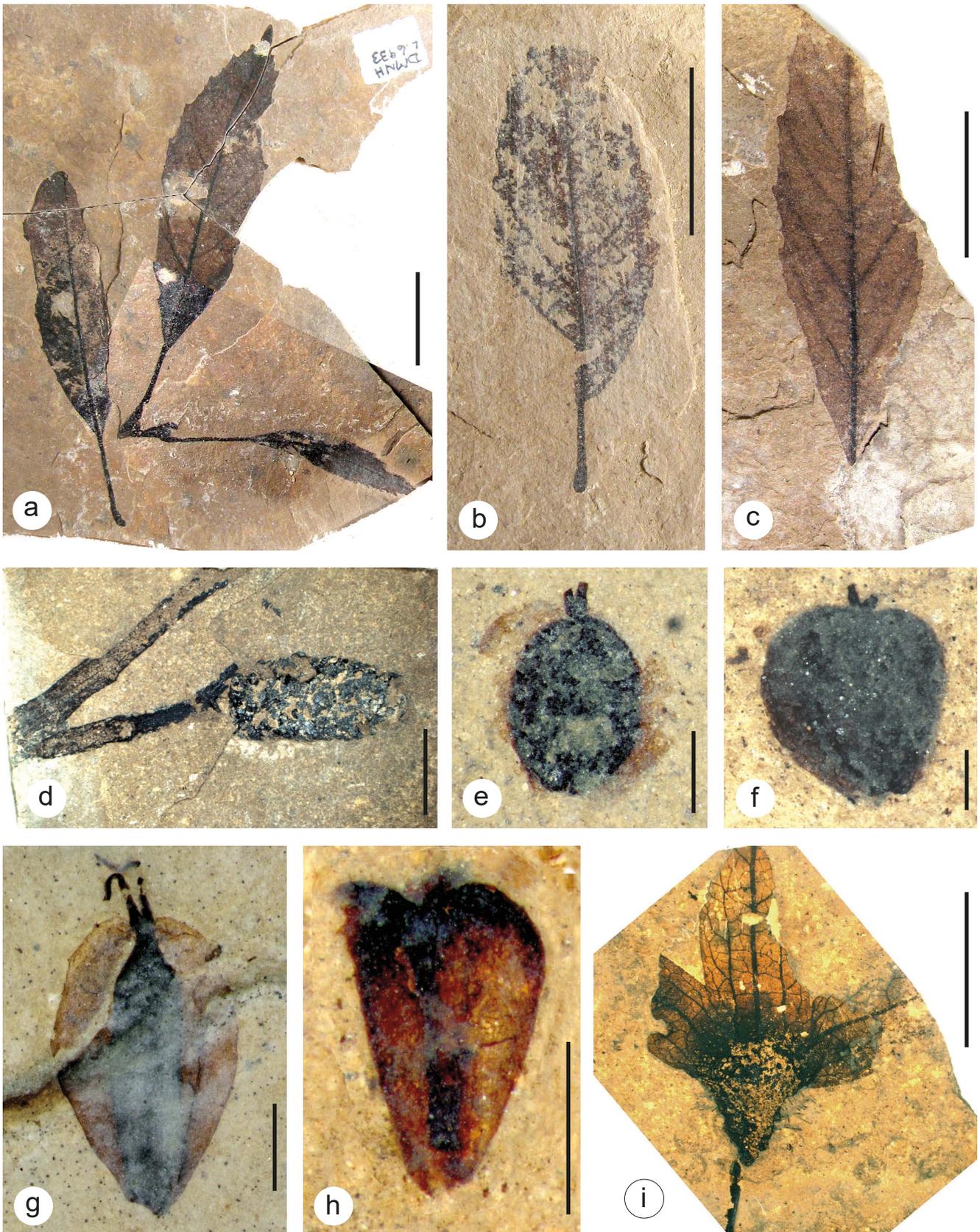
Genus *Palaeocarya* SAPORTA

Text-fig. 8i

Material. USNM PAL 622690.

Locality. Disbrow Creek.

Description. Winged fruit incomplete, 2.1 cm long and 1.7 cm wide; main wing trilobed; lobes lanceolate



Text-fig. 8. Betulaceae and Juglandaceae from the Kishenehn Formation. a: DMNH L6933 *Alnus* sp. L1 leaves. Scale bar 2 cm. b: DMNH EPL.48179 *Alnus* sp. leaf. Scale bar 2 cm. c: DMNH EPL.48136b *Alnus* sp. leaf. Scale bar 2 cm. d: USNM PAL 622756 *Alnus* sp. I1 infructescence attached to branch. Scale bar 1 cm. e: USNM PAL 623160 Betuloideae showing wing, seed body and two persistent styles. Scale bar 1 mm. f: USNM PAL 622732 *Alnus* sp. F1 samara showing two persistent styles. Scale bar 1 mm. g: USNM PAL 624925 *Betula* sp. samara showing wing, seed body and two persistent styles. Scale bar 1 mm. h: USNM PAL 623147 *Alnus* sp. F2 samara showing. Scale bar 1 mm. i: USNM PAL 622690 *Palaecocarya* sp. samara showing three wings with reticulate venation and hairs at base. Scale bar 1 cm.

diverging at 46.4°, middle lobe 7.0 mm wide and lateral lobes 5.4–5.8 mm wide; wing lobes possessing three main veins, each with the midvein being the thickest; lateral ascending veins dissipate into loops distally, epimedial veins mostly perpendicular, exmedial veins branching apically, veins visible up to third order. Prophyllum ca. 0.8 cm long and 0.6 cm wide with straight, unbranched trichomes below the wing measuring between and 1.7 to 3.7 mm long.

Remarks. *Palaeocarya* is a fossil genus that accommodates fruits with trilobed wings, similar to those of the extant genera, *Engelhardia* LESCH. ex BLUME of Asia and *Oreomunnea* of Central America. Distinctions between species of the extant genera and in *Palaeocarya* can be made in part by wing venation patterns (Manchester 1987). Only the basal portions of the wings are seen in this specimen. *Palaeocarya clarnensis* MANCHESTER and *P. uintaensis* (MACGINITIE) MANCHESTER both appear to have three main veins in the basal portion of their wings, however, the lateral veins of *P. uintaensis* become secondary loops more apically (Manchester 1987) whereas *P. clarnensis* has a pubescent nutlet base (Manchester 1987) like this fossil. Because this fossil shares features of both species and *P. uintaensis* is known from only one specimen, this fossil is not being assigned to a species. More specimens may help resolve its taxonomic affinity. *P. clarnensis* has been observed in collections from the Green River Formation (Little Mountain, Wyoming) as well as from the Clarno Formation (West Branch Creek and Gosner Road, Oregon), with the Clarno localities being a similar age to the Kishenehn Formation (Manchester 1987). *P. uintaensis* is known only from the Green River Formation (Rainbow, Utah) (MacGinitie 1969, Manchester 1987).

Family Betulaceae GRAY
Subfamily Betuloideae KOEHNE

Betuloideae sp.

Text-fig. 8e

Material. USNM PAL 623160.

Locality. Disbrow Creek.

Description. Fruit a samara, circular in outline, 2.5 mm tall, 2.4–2.6 mm wide; seed body elliptical, in center of fruit, 2.1 mm tall, 1.6 mm wide; styles two, persistent, 0.4 mm tall and 0.1 mm wide with flat stigmas.

Remarks. The specimen has a thin, differentiated wing as in most *Betula* species but has stout styles as in most *Alnus* species.

Genus *Alnus* MILL.

***Alnus* sp. II**

Text-fig. 8d

Material. USNM PAL 622756.

Locality. Disbrow Creek.

Description. Infructescence cylindrical, 14.7 mm long, 7.1 mm wide; borne on a twig 1.2–3.8 mm wide.

Remarks. Although the attachment is not completely preserved, it appears that the peduncle on this specimen was

short. Due to the thick, coalified bracts, this specimen likely belongs to *Alnus* rather than *Betula*, which has thinner, deciduous bracts.

Genus *Alnus* MILL.

***Alnus* sp. F1**

Text-fig. 8f

Material. USNM PAL 622732, 626069.

Locality. Deep Ford and Disbrow Creek.

Description. Seed body obovate 2.7–2.8 mm tall, 2.4–2.6 mm wide; base concave; apex retuse; two styles 0.3–0.4 mm tall, 0.1–0.2 mm wide with flat stigmas.

Remarks. These two specimens have wings that are not well differentiated from the seed body and have stout styles which resemble some species of *Alnus*.

***Alnus* sp. F2**

Text-fig. 8h

Material. USNM PAL 623147.

Locality. Disbrow Creek.

Description. Seed body obovate 1.8 mm tall, 1.3 mm wide at widest; apex retuse; stylar base(s) present, 0.2 mm tall, 0.2 mm wide.

Remarks. The seed is smaller than *Alnus* sp. F1 and has a thinner wing but still not as defined from the seed body as in most species of *Alnus*.

***Alnus* sp. L1**

Text-fig. 8a–c

Material. DMNH L6933, DMNH EPI.48136a&b, DMNH EPI.48179.

Locality. Dishbrow Creek.

Description. Leaves simple, elliptical, 5.5–9.2 cm long, 0.7–2.2 mm wide; base and apex acute; petioles 1.6–2.2 cm long, 0.8–1.1 mm wide; venation pinnate, secondaries arising decurrently, arising at 51° craspedodromous, entering sinuses of large teeth; 0.84 secondaries/cm; tertiary veins percurrent, opposite and alternate; higher venation not visible; teeth compound, with one large and or two small teeth; large teeth with retroflexed proximal flank, rounded apex and straight distal flank; smaller teeth with concave proximal and distal flanks with acute or rounded apices; 2.68 teeth per cm.

Remarks. *Alnus* is a microthermal taxon that can be found in riparian areas (Wing 1987). Fossils of *Alnus* are known from the early Eocene McAbee, Quilchena and Falkner floras of British Columbia (Lowe et al. 2018, Mathewes et al. 2016, Smith et al. 2012), Republic flora of Washington (Pigg et al. 2011), Yellowstone flora of Wyoming (Wing 1987), the Golden Valley Formation of North Dakota (Hickey 1977, Wing 1987), mid-Eocene Thunder Mountain flora of Idaho (Axelrod 1998), White Cliffs flora of the Clarno Formation of Oregon (Liu et al. 2014), late Eocene Copper Basin flora of Nevada (Wing 1987), Bull Run flora of Nevada (Wing 1987), Whitecap Knoll flora of the John

Day Formation, Oregon (Manchester 2000) and Oligocene Ruby Basin of Montana (Becker 1959).

Genus *Betula* L.

***Betula* sp.**

Text-fig. 8g

Material. USNM PAL 624925.

Locality. Dakin.

Description. Samara obovate 4.0 mm long, 2.2 mm wide; seed body in center of wing, fusiform 3.0 mm long, 0.8 mm wide; style splits near margin of wing 1.3 mm long, curled; wing 0.6 mm wide and tapers at base.

Remarks. The thin wing that is differentiated from the seed body and long styles of the seed distinguish this specimen as *Betula* and can be contrasted with the non-differentiated wing and short styles in *Alnus*. *Betula* fossils are known from the early Eocene McAbee, One Mile Creek, Quilchena and Falkland floras of British Columbia (Crane and Stockey 1987, Lowe et al. 2018, Mathewes et al. 2016, Smith et al. 2012), Republic flora of Washington (Wolfe and Wehr 1987, Pigg et al. 2011) and late Eocene Bull Run flora of Nevada (Wing 1987). *Alnus* appears to be more common in Paleogene deposits compared to *Betula*, which may be due to temperature or its proximity to the water (pers. obs.).

Family Sapindaceae Juss.

Genus *Dipteronia* OLIV.

Text-fig. 9a

Material. USNM PAL 625742.

Locality. Spring.

Description. Samara 15.0 mm tall, 10.5 mm wide; pedicel 4.4 mm long, 0.4 mm wide; disc 0.5 mm tall, 1.7 mm wide; abortive fruit 1.1 mm in diameter; laminated vascular bundle emerging out of disc and into flat, circular seed body 1.0 mm in diameter, surrounded by circular wing 5.2 mm in diameter; veins radiate from center, dichotomizing occasionally between margin or halfway between margin and seed body; fimbrial vein surrounds wing.

Remarks. The presence of a hypogynous perianth and disc scar at the junction of the pedicel and fruit and shape of the samara conform to *Dipteronia*. Fimbrial veins may be absent in *Dipteronia* fruit such as *Dipteronia sinensis* OLIV. or present such as in *Dipteronia dyeriana* HENRY and *Dipteronia brownii* McCLAIN et MANCHESTER (McClain and Manchester 2001). *Dipteronia* fruits are known from the Paleocene of Wyoming, the middle and late Eocene of British Columbia, Washington, Oregon and Colorado and the early Oligocene of Oregon (McClain and Manchester 2001), as well as from the early Oligocene of western China (Ding et al. 2018).

Genus cf. *Boniodendron* GAGNEP.

Text-fig. 9b

Material. USNM PAL 621805.

Locality. Disbrow Creek.

Description. Portion of membranous capsular fruit, 7.8 mm wide divided by a line of dehiscence; veins dichotomizing and anastomosing forming 2–5 elliptical regions before terminating in a fimbrial vein.

Remarks. Our specimen shows similarities to those which Becker (1961) described as *Koelreuteria* MEDIK. from the Oligocene of Ruby River Basin, Montana. Although fossils of *Koelreuteria* are also known from the early Eocene Republic flora of Washington, Wang et al. (2013) recommend using cf. *Boniodendron* for the Ruby River Basin fossil in addition to similar fossil fruits found at Republic because they are half the size of *Koelreuteria* and have complete septa.

Family Sapindaceae Juss.

Sapindaceae sp.

Text-fig. 9c

Material. USNM PAL 625792.

Locality. Spring.

Description. Fruit a bladder-like capsule, elliptical, 17.2 mm tall with three wings showing, each 6.8 mm wide, divided by a line of dehiscence; seeds circular, 1.0 mm long to 0.7 mm wide; one per locule attached near the midway point between base and apex of the fruit.

This faintly preserved specimen shows quite clearly the longitudinal septum and darkened central seed attachments, but the outline of the surrounding bladder is seen only near the base and apex. The septa in *Koelreuteria* (Sapindaceae), terminate, distally about a third of the way up the fruit, where the seeds attach (Manchester et al. 2009), so that the locular cavities join into a single locule above the seed attachment. Our specimen does not show termination in the septa. Neither *Craigia* W.W.SM. et W.E.EVANS (Malvaceae), *Urvillea* KUNTH (Sapindaceae) nor *Arfeuillea* PIERRE ex RADLK. (Sapindaceae) possess this feature of our fossil. Species of *Craigia* vary in length from 9–35 mm and 7–33 mm in width, are septicial and possess wings with radiating veins (Wang et al. 2021). *Urvillea* is 20–40 mm tall 15–18 mm wide (in *U. venezuelensis* FERRUCCI), is septifragal, one-seeded, has sub-parallel veins and its veins radiate outward (Ferrucci 2006, Wang et al. 2013, 2021). *Arfeuillea* is 50 mm long, 45 mm wide, is loculicidal and has net-like veins and a flat to slightly rounded apex. cf. *Boniodendron* is a potential candidate as the modern fruits are subglobose, 18–23 mm tall and have one seed per locule at the same level as in this fossil (Wang et al. 2013). *Boniodendron* has loculicidal dehiscence (Wang et al. 2013). Without a clear understanding of how the valves open or the venation, we are unable to assign this fossil to a genus. Based on the commonality of winged-bladder fruits in Sapindaceae, the fossil likely belongs to this family.

Family Simaroubaceae DC.

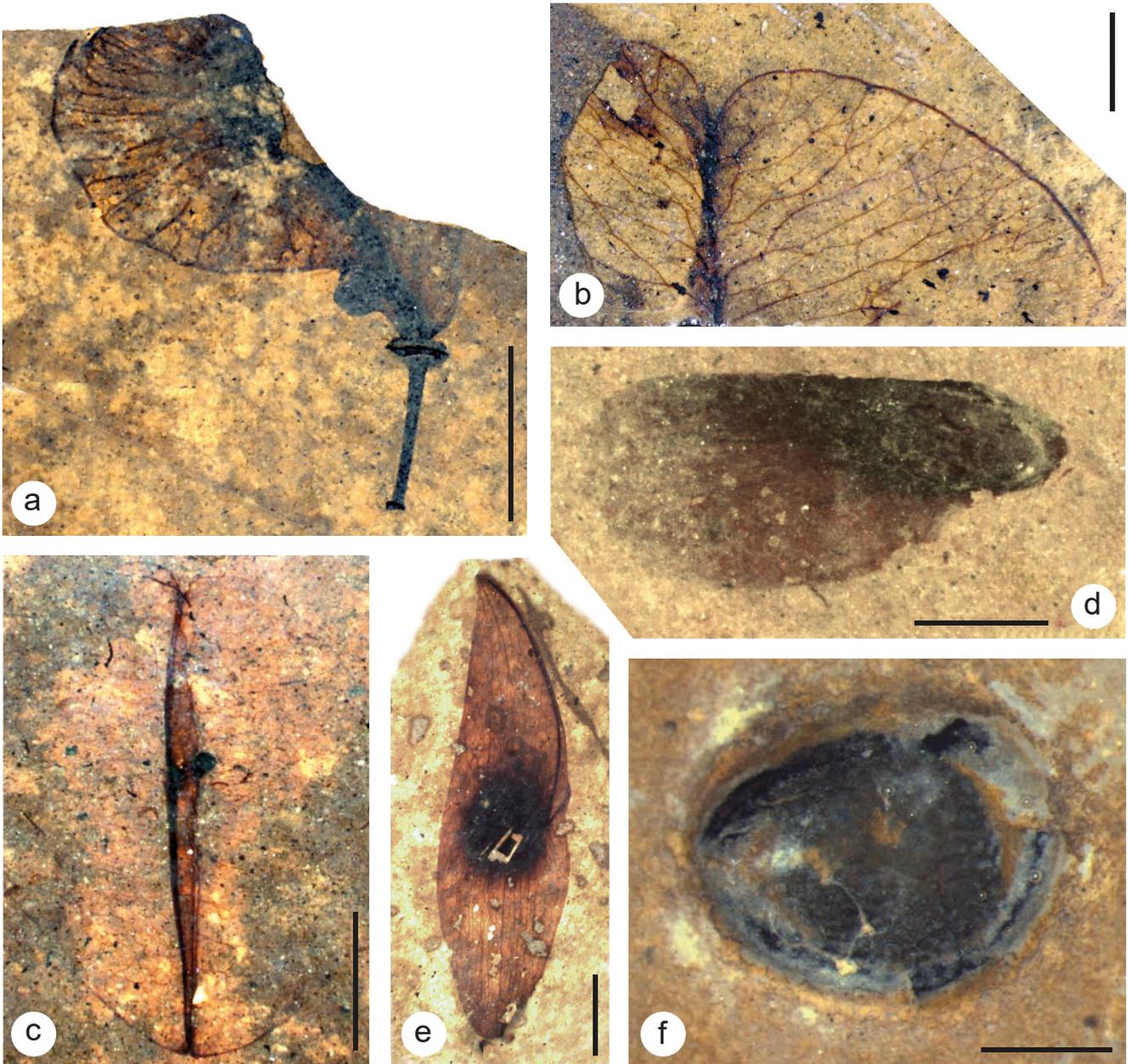
Genus *Ailanthus* DESF.

***Ailanthus confucii* UNGER**

Text-fig. 9e

Material. USNM PAL 622108, 622276, 622650.

Locality. Disbrow Creek.



Text-fig. 9. a: USNM PAL 625742 *Dipteronia samara* showing pedicel, disc, an undeveloped fruit and a developed fruit. Scale bar 5 mm. b: USNM PAL 621805 wings of cf. *Boniodendron capsulae*. Scale bar 2 mm. c: USNM PAL 625792 Sapindaceae capsular fruit with wings, septae and seeds. Scale bar 5 mm. d: USNM PAL 623735 cf. *Cedrela* seed. Scale bar 3 mm. e: USNM PAL 622276 *Ailanthus confucii* fruit showing seed body, ventral vein and stylar vein. Scale bar 5 mm. f: USNM PAL 624113 *Rutaspermum* sp. Scale bar 2 mm.

Description. Winged fruit elongate-elliptical, with a central seed body; wing with pointed apex and base; fruit 25.1–32.12 mm long, 7.3–8.6 mm wide; seed body 4.9–6.4 mm long, 3.7–5.3 mm wide; ventral (intramarginal) vein of the wing prominent, marginal or submarginal; stylar vein present, minor vein small, mostly parallel, occasionally dichotomizing or anastomosing (more on dorsal side); seed bodies sub-circular.

Remarks. *Ailanthus* fruits in North America have traditionally been placed into either *Ailanthus americana* COCKERELL or *Ailanthus lesquereuxi* COCKERELL but are morphologically identical to those described earlier as *Ailanthus confucii* UNGER (Corbett and Manchester 2004). The fossil matches the description of *A. confucii* by having

a marginal to submarginal ventral vein as opposed to having an inset vein as in *Ailanthus tardensis* HABILY (Corbett and Manchester 2004). *A. confucii* is recognized from the early Eocene through late Miocene of western North America (Corbett and Manchester 2004). Among extant species, it resembles the temperate eastern Asian native species, *Ailanthus altissima*, which is invasive today in North America and Europe.

Family Meliaceae JUSS.
Genus cf. *Cedrela* P.BROWNE
 Text-fig. 9d

Material. USNM PAL 623735.

Locality. Dakin.

Description. Winged seed at least 7.5–10.8 mm long, 3.4–4.9 mm wide at widest; seed body elliptical, on proximal side of wing, long axis of seed body almost parallel to wing, pointing slightly ventrally, 2.5–3.4 mm long, 1.3–2.1 mm wide; wing extending around whole seed body becomes wider halfway down seed body and becomes widest past the distal pole where it maintains width; wing contains small, straight striations that run parallel to the course of the wing.

Remarks. We were unable to observe the cellular pattern of the wing so are hesitant to place it firmly in the genus *Cedrela* because similar veinless single-winged seeds occur in many other taxa (for listing of examples, see Kvaček and Wilde 2010). *Cedrela* is reported from the early Eocene Kisinger Lakes and (rarely) in the Green River Formation, late Eocene Florissant Formation of Colorado (MacGinitie 1953) and early Oligocene Bridge Creek flora of the John Day Formation, Oregon (Meyer and Manchester 1997). *Cedrela*-like seeds are known from the late Eocene Whitecap Knoll flora of the John Day Formation, Oregon but differ in wing cell pattern (Manchester 2000).

Family Rutaceae JUSS.
Genus *Rutaspermum* CHANDLER
Text-fig. 9f

Material. USNM PAL 624113.

Locality. Dakin.

Description. Seed ovate 2.8 mm long, 2.1 mm wide at widest point with elongate lateral hilum 0.7 mm long; reticulate to punctate sculpture with round fossae.

Remarks. The fossil genus *Rutaspermum* is used for seeds with rutaceous affinity that cannot be placed into a modern genus. Whereas our seed has a similar shape to other *Rutaspermum*, the sculpture is more pronounced in our fossil (Gregor 1989). Modern rutaceous genera such as *Zanthoxylum* can extend from subtropical into temperate latitudes (eFloras 2008–2022).

Family Brassicaceae BURNETT.
Genus *Thlaspi* L.
Text-fig. 10a–h

Material. USNM PAL 622306, 623124, 623138 and DMNH EPI.41847, 48190, 48216, 48222, 48239.

Locality. Disbrow Creek.

Description. Winged capsular fruit 14.3 mm long, 9.2 mm wide; pedicel 2.9 mm long; pedicel truncated; wing elliptical to ovate, with a rounded base and emarginate apex; approximately 2.5 mm between edge of central body and wing margin; fimbrial vein present; veins arise between 38–46°. Arching apically about half-way, occasional bifurcations with the apical vein retaining the same thickness; veins lose thickness towards margin; central locular area thicker/darker than surrounding wing, fusiform, 7.2 mm long, 3.1 mm wide with longitudinal groove, slit or suture running the entire length; persistent styles 1.3 mm long; wing surrounds two styles.

Remarks. We considered various candidate families for the identification of these winged fruits before settling on the assignment to *Thlaspi* in the Brassicaceae. The fossils are distinctive in the presence of a central body, persistent styles and arching veins of the wings. The dispersed valves of *Koelreuteria* LAXM. (Sapindaceae) and *Craigia* W.W.SM. et W.E.EVANS (Malvaceae) capsular fruits also have bilateral symmetry and are known from Eocene deposits of North America (Kvaček et al. 2005, Wang et al. 2013). *Craigia* can be distinguished from *Koelreuteria* by the presence of a fusiform central locule in the former (Wang et al. 2013). Two species of *Craigia* are currently recognized, *Craigia bronni* (UNGER) KVAČEK, BŮŽEK et MANCHESTER from Europe and western Asia and *Craigia oregonensis* (ARNOLD) KVAČEK, BŮŽEK et MANCHESTER from North America and Asia (Kvaček et al. 2005). These fruits have straight veins that do not lose gauge towards the wing margin unlike the fossil (Kvaček et al. 2005). We also considered the families Begoniaceae C.AGARDH and Polygonaceae JUSS. The sides of the proximal portion of the central body in *Begonia* L. is detached from the wing but the overall shape is obovate and there is persistent stamen and style (Manchester and O’Leary 2010). The wings on polygonaceous fruit are derived from the perianth and possess thin veins (Manchester and O’Leary 2010).

The venation pattern, locule shape, persistent pedicel and style of these specimens are consistent with the previously described fossil *Thlaspi primaevum* H.F.BECKER from the early Oligocene Ruby flora from western Montana (Becker 1961, Beilstein et al. 2010). We also compared the specimen to *Noccaea* MOENCH but the veins of that genus are less defined than those in *Thlaspi*. The wings of *Thlaspi primaevum* do not fully surround the stylar area and the perianth scars are more pronounced (Becker 1961, Manchester and O’Leary 2010). This fossil from the Kishenehn is the oldest occurrence of *Thlaspi*. It would imply still an earlier radiation of the clade that includes *Arabidopsis* (Beilstein et al. 2010). The type species, *T. arvense* L., has a similar wing morphology, with the wings encompassing the stylar area, though the central body appears to be proportionally wider.

Family Amaranthaceae JUSS.
Genus *Chenopodium* L.
***Chenopodium* sp. 1**
Text-fig. 11a

Material. USNM PAL 624090.

Locality. Dakin.

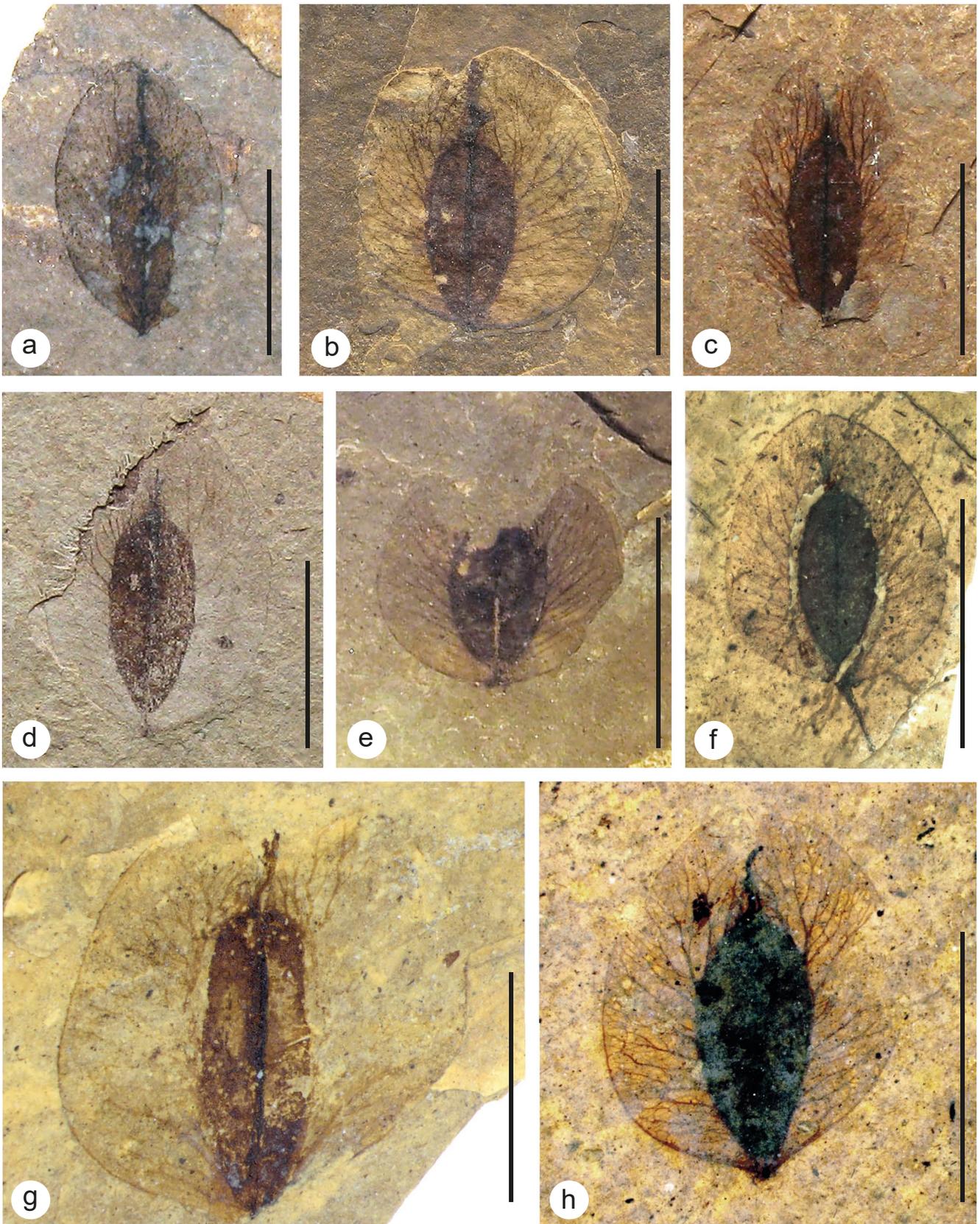
Description. Seed circular, curved embryo, 1.3 mm long, 1.1 mm wide; eight rows of circular, concentric reticulae; hilar region 0.3 mm long, 0.1 mm deep; persistent funicle 0.1 mm wide, 0.1 mm wide.

***Chenopodium* sp. 2**
Text-fig. 11b

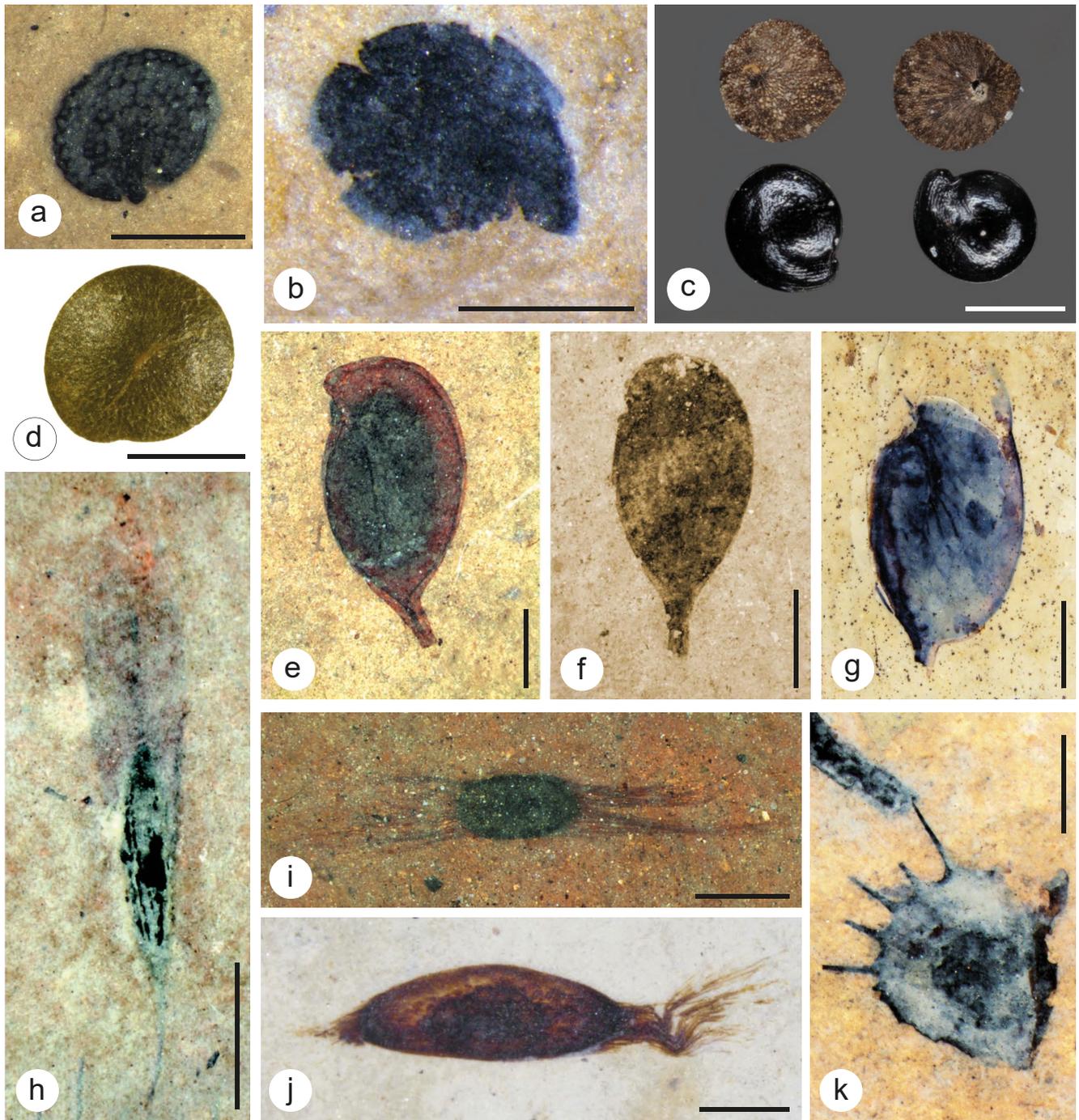
Material. USNM PAL 624372.

Locality. Dakin.

Description. Seed circular, 1.4–1.2 mm in diameter, funicle 0.3 mm long, 0.3 mm wide, sculpture psilate.



Text-fig. 10. Winged capsules of *Thlaspi* sp. fruits from the Kishenehn Formation. a: DMNH EPL.48222 *Thlaspi* sp. winged capsule showing fusiform central seed body and venation in wing. Scale bar 1 cm. b: DMNH EPL.48216 *Thlaspi* sp. winged capsule showing fusiform central seed body and venation in wing and persistent style. Scale bar 1 cm. c: DMNH EPL.48190 *Thlaspi* sp. winged capsule showing fusiform central seed body and venation in wing. Scale bar 1 cm. d: DMNH EPL.48239 *Thlaspi* sp. winged capsule showing fusiform central seed body and venation in wing. Scale bar 1 cm. e: DMNH EPL.41847 *Thlaspi* sp. winged capsule. Scale bar 1 cm. f: USNM PAL 622306 *Thlaspi* sp. winged capsule showing pedicel, fusiform central seed body and venation in wing. Scale bar 1 cm. g: USNM PAL 623138 *Thlaspi* sp. winged capsule showing fusiform central seed body, persistent styles and venation in wing. Scale bar 1 cm. h: USNM PAL 623124 *Thlaspi* sp. winged capsule showing fusiform central seed body, persistent styles and venation in wing. Scale bar 1 cm.



Text-fig. 11. a: USNM PAL 624090 *Chenopodium* sp. 1. Scale bar 1 mm. b: USNM PAL 624372 *Chenopodium* sp. 2. Scale bar 2 mm. c: *Chenopodium pratericola* from Minnesota Wildflowers 2023b. d: *Chenopodium hybridum*, FLAS seed collection. Scale bar 1 mm. e: USNM PAL 625523 *Eucommia montana* showing subapical stigmatic cleft, seed body and stipe. Scale bar 1 mm. f: USNM PAL 625160 *E. montana* showing faint subapical stigmatic cleft and stipe. Scale bar 2 mm. g: USNM PAL 768185 *E. montana* showing subapical stigmatic cleft, reticulate venation and stipe. Scale bar 2 mm. h: USNM PAL 624697 *Fraxinus* sp. samara showing long persistent pedicel, seed body and wing. Scale bar 5 mm. i: USNM PAL 625396 Catalpae seed with frayed wings. Scale bar 2 mm. j: USNM PAL 624316 Catalpae seed with frayed wings. Scale bar 1 mm. k: USNM PAL 722179 Apialean schizocarp with lateral spines and line of dehiscence. Scale bar 2 mm.

Comments on *Chenopodium*

Chenopodium seeds are round with a funicle and range in sculpture from reticulate to psilate (Benet-Pierce and Simpson 2014). A reticulate sculptured *Chenopodium* is known from the Miocene-Pleistocene of Tibet, however, *Chenopodium* sp. 1 has larger fossa in the reticulae and *Chenopodium* sp. 2 is psilate (Huang et al. 2021). Modern *Chenopodium* seeds can be reticulate or psilate (Benet-Pierce and Simpson 2014).

Here we figure *Chenopodium pratericola* RYDB. (Text-fig. 11c, Minnesota Wildflowers 2023b) and *Chenopodium polyspermum* L. (Text-fig. 11d, Agricultura Romanaeasca 2011) as comparisons. We also compared these two seeds to those of *Corydalis* DC. (Papaveraceae) which are of similar size, shape and may be reticulate or psilate. It would appear though that *Corydalis* seeds are slightly less circular and have a deeper indentation near the funicle (pers. obs.).

Rutaspermum was also identified from the Kishenehn but we distinguish these *Chenopodium* from the *Rutaspermum* by their circular rather than reniform shape. *Eurya* THUNB. (Theaceae) is also reniform (Bhandari et al. 2009). We also looked at other genera in the Chenopodioideae. *Stutzia* E.H.ZACHARIAS has fruiting bracts that are arrowhead shaped (Zacharias 2012). *Cycloloma* fruits generally have attached, papery perianth, and although that could have worn off to leave the seed, the hilar scar is less prominent (image by Carole Ritchie, United States Department of Agriculture Natural Resource Conservation Service PLANTS Database in Vescovo 2023). Both *Chenopodiastrum* S.FUENTES and *Cycloloma* appear less coiled than *Chenopodium* (image by Stefan Lefnaer in Areces-Berazain 2022, image by Carole Ritchie, United States Department of Agriculture Natural Resource Conservation Service PLANTS Database in Vescovo 2023). This is not an exhaustive list of genera in Chenopodioideae but should serve to illustrate that these seeds are distinguishable from other dissimulans in the subfamily. These are the oldest recorded *Chenopodium* fossils.

Family Eucommiaceae ENGL.

Genus *Eucommia* OLIV.

***Eucommia montana* R.W.BR.**

Text-fig. 11e–g

Material. USNM PAL 717259, 622651, 623020, 623513, 624027, 624249, 624336, 624374, 624717, 624808, 717508, 625160, 625523, 625756, 768185.

Localities. Dakin, Disbrow Creek, Park and Spring.

Description. Samaras 1.6–8.9 mm long to 0.7–4.5 mm wide; endocarp 1.0–6.5 mm long to 0.6–3.2 mm wide; fruits and seed bodies elliptical with seed bodies in the center of the samara; reticulate venation over the endocarp and a strong intramarginal or marginal vein along the wing margins; stigmatic cleft, positioned laterally near the apex; basal stipe present.

Remarks. Size and length width ratios are the key distinguishing factors for fossil *Eucommia* species endemic to east Asia (Call and Dilcher 1997, Manchester et al. 2009). These fossils fall within the size ranges of *Eucommia montana* which displays a wide range (Becker 1969, Call and Dilcher 1997). *Eucommia montana* is known from the early Eocene to Oligocene as far north as Quilchena, British Columbia and as far south and east as Florissant, Colorado (Call and Dilcher 1997). This species had smaller fruits than those known from the Eocene of Mississippi (Call and Dilcher 1997) and Oligocene of southern Mexico (Magallón-Puebla and Cevallos-Ferriz 1994). *Eucommia* is now endemic to China, but its fossil record includes North American and European as well as Asian occurrences (Manchester et al. 2009).

Family Oleaceae HOFFMANNS. et LINK

Genus *Fraxinus* L.

***Fraxinus* sp.**

Text-fig. 11h

Material. USNM PAL 624697.

Locality. Dakin.

Description. Samara 1.5 cm long and 0.3 cm wide, elongated obovate; pedicel 0.4 cm long; seed body fusiform 0.7 cm and long 0.1 cm wide (L/W ratio 5.38) oriented so the long axis is in the long axis of the fruit; fruit length/seed length ratio 2.89; vein running from the apex of seed body to the distal end of fruit; calyx absent.

Remarks. Wu et al. (2021) determined that length/width ratios of the fruit and seed bodies in addition to the fruit length to seed length can help with diagnosing sections within *Fraxinus*. Although the distal end of this fruit is missing, the fruit L/W ratio has to be greater than 4.5 and the fruit length/seed length ratio has to be greater than 2.19. These ratios would place our *Fraxinus* into section *Melioides* or section *Fraxinus* (Wu et al. 2021). Mathewes et al. (2021) reviewed Eocene fossil *Fraxinus* fruits from the Eocene Quilchena locality in British Columbia. Our fossil bears some resemblance to the samaras in their pl. II, fig. 2, with narrow bases that lack a calyx (Mathewes et al. 2021).

Family Bignoniaceae JUSS.

Catalpeae DC. ex MEISN.

Catalpeae sp.

Text-fig. 11i, j

Material. USNM PAL 624316, 625396, 624316.

Localities. Dakin and Spring.

Description. Bi-winged seed, 5.9–10.2 mm long, 1.1–1.4 mm wide; distal wing margin hairy; wings never wider than central body; central body 3.0 mm long; seed elliptical, 1.3–2.6 mm long 0.6–1.4 mm wide.

Remarks. Bi-winged seeds are characteristic of many Bignoniaceae. The tribe Catalpeae DC. ex MEISN. includes the extant genera *Catalpa* SCOP. and *Chilopsis* D.DON, which both have distally shredded seed wings (Lersten et al. 2002). We choose to point out this similarity instead of placing our specimens in Catalpeae, out of caution, because we have not conducted a full survey of the family; other bignoniaceous tribes might also have distally shredded seed wings.

Order Apiales NAKAI

Apiales sp.

Text-fig. 11k

Material. USNM PAL 722179.

Locality: Disbrow Creek.

Description. Schizocarpic achene; flat proximal edge and rounded distal edge, 4.3 mm tall, 3.6 mm wide (excluding spines); six lateral spines on distal apical end measuring between 0.6 and 1.5 mm long.

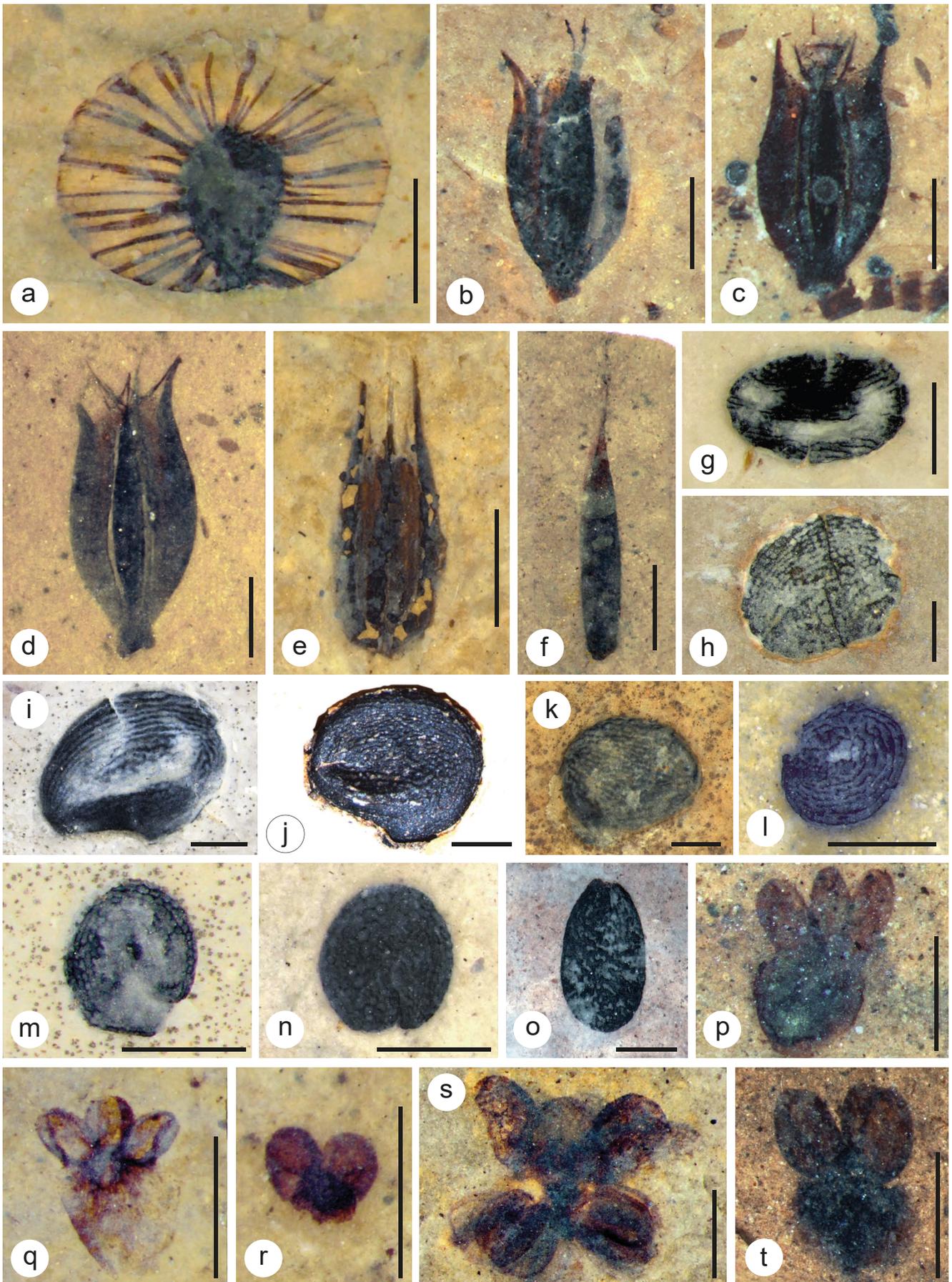
Remarks. Spiny achenes close in size and shape are found in *Hydrocotyle* L. (Araliaceae JUSS.) (e.g., *H. scutellifera* BENTH.) (Perkins 2019) and Apiaceae.

Incertae sedis

Genus *Pteroheterochrosperma* gen. nov.

Type. *Pteroheterochrosperma horseflyensis* sp. nov.

Plant Fossil Names Registry. PFN003030 (for new genus).



Text-fig. 12. a: USNM PAL 722530 *Pteroheterochrosperma horseflyensis* gen. et sp. nov. SMITH et MANCHESTER. Scale bar 2 mm. b: USNM PAL 622695 *Quadrasubulaflora kishenehnensis* gen. et sp. nov. SMITH et MANCHESTER showing three outer parts and two stigma. Scale bar 1 mm. c: USNM PAL 625447 *Q. kishenehnensis* showing three outer parts. Scale bar 1 mm. d: USNM PAL 624649 *Q. kishenehnensis* showing three outer parts. Scale bar 1 mm. e: USNM PAL 622402 *Q. kishenehnensis*. Scale bar 2 mm. f: USNM

Generic diagnosis. Winged structure circular with dark, thick striations radiating around obovate seed body, seed body with rugulate sculpture.

Etymology. The genus is Greek for “variegated winged seed” with “ptero-” for “wing”, “-heterochros-” for “variegated” and “-sperma” for “seed”.

Remarks on genus. One species in newly erected genus, preserved on tan-gray paper-shale.

***Pteroheterochrosperma horseflyensis* sp. nov.**

Text-fig. 12a

Plant Fossil Names Registry. PFN003031 (for new species).

Etymology. The specific epithet is for the Horsefly, British Columbia where the first fossils of this species were described.

Holotype. USNM PAL 722530, National Museum of Natural History, District of Columbia, USA, Text-fig. 12a.

Type horizon and type locality. Dakin Site in the Kishenehn Formation, ca. 44 Ma.

Specific diagnosis. Winged structure circular; wing has thick striations (up to 0.1 mm) radiating around seed body starting from the seed body and mostly terminating at the margin of the wing, some striations bifurcating; seed body obovate with rugulate sculpture.

Size. Structure 2.1 mm tall, 2.7 mm wide; seed body 1.28 mm tall, 0.77 mm wide.

Description. Roughly 27 striations radiating from the seed body, some bifurcating or trifurcating.

Remarks. Similar disseminules have been found from the early Eocene Okanogan sites of Republic, WA (Pigg and Wehr 2002), McAbee, BC and Horsefly, BC (UWBMB4131-96008, DSCN6543). Penhallow (1908) assigned specimens from Horsefly of this disseminule as *Ulmus minuta* GOEPP. (94–95), which was a leaf species, but he recognized that the fruit was much smaller than other known fossil and modern elms. *U. minuta* is a synonym for *Ulmus pyramidalis* (GOEPPERT) emend. ILJINSK. (Takhtajan 1982, Traiser et al. 2019). *U. pyramidalis* DIPPEL was already in use for a different extant elm and was recognized as a synonym of *Ulmus glabra* HUDS. *U. glabra*'s modern geographic range includes Europe and western Asia but its fruits lack the thick, darkened veins that appear in the fossil and possess two styles which the fossil lacks (Thomas et al. 2018, Sherman-Broyles 2021). These tiny disseminules lack the wing venation and stylar cleft and style diagnostic for *Ulmus*, and thus require a new binomial.

Genus *Quadrasubulaflora* gen. nov.

Type. *Quadrasubulaflora kishenehnensis* sp. nov.

Plant Fossil Names Registry. PFN003032 (for new genus).

Generic diagnosis. Epigynous flower square in cross section with awl-shaped projections in each corner beginning at the base above the pedicel, connected by a lamina; base flat to slightly rounded; center with hair-like projections.

Etymology. The genus is Latin for “four awl flower” (“quadra-” for “four”, “-subula-” for “awl” and “-flora” for “flower”).

Remarks on genus. One species in newly erected genus, preserved on tan-gray paper-shale.

***Quadrasubulaflora kishenehnensis* sp. nov.**

Text-fig. 12b–e

Plant Fossil Names Registry. PFN003033 (for new species).

Etymology. The specific epithet is for the for the Kishenehn Formation.

Material. USNM PAL 624649, 625447, 622695, 622402, 623987, 624154.

Holotype. USNM PAL 625447, National Museum of Natural History, District of Columbia, USA, Text-fig. 12c.

Type horizon and type locality. Spring Site in the Kishenehn Formation, ca. 44 Ma.

Other localities. Dakin, Dishbow Creek and Spring Sites.

Specific diagnosis. Flower square in cross section, elliptical in longitudinal section; pedicel slightly curved; awl-shaped and apices point outward with concave calyx lamina curving up to connect corners; hair-like projections protruding from near the axis.

Size. Flower 1.5–2.2 mm diagonal cross section, each side 1.0–1.5 mm long, 2.9–5.1 mm tall; pedicel 0.2–0.3 tall, basal corners of flower protrude outward 0.3–0.4 mm wide; hair like projections 0.5–0.8 mm long.

Description. Hair-like projections are in the same plane as the corners of the flower.

Remarks. Possible affinities for this structure are flowers or fruits in tribe Saniculeae and tribe Scandiceae subtribe Scandicinae in Apiaceae because of their shape, size and projections.

PAL 722210 “KF1”. Scale bar 2 mm. g: USNM PAL 624877 KF2. Scale bar 1 mm. h: USNM PAL 624832 KF3. Scale bar 2 mm. i: USNM PAL 768303 KF4. Scale bar 1 mm. j: USNM PAL 625629 KF4. Scale bar 3 mm. k: USNM PAL 624455 KF5. Scale bar 3 mm. l: USNM PAL 609598 KF6 seed. Scale bar 1 mm. m: USNM PAL 722298 KF7. Scale bar 1 mm. n: USNM PAL 625631 KF7. Scale bar 1 mm. o: USNM PAL 625736 KF8. Scale bar 2 mm. p: USNM PAL 625551 KF9 Scale bar 1 mm. q: USNM PAL 621685 KF9. Scale bar 1 mm. r: USNM PAL 620311 KF9. Scale bar 1 mm. s: USNM PAL 626216 KF9. Scale bar 1 mm. t: USNM PAL 625608 KF9. Scale bar 1 mm.

Taxon KF1

Text-fig. 12f

Material. USNM PAL 621406, 623148, 623158, 722210.

Localities. Disbrow Creek and Park.

Description. Samara lanceolate, 9.7 mm long, 0.9–1.2 mm wide at widest point; proximal end curved, distal end pointed; seed body lanceolate with curved proximal end and pointed distal end, 4.7–6.6 mm long, 0.9–1.2 mm wide at widest.

Taxon KF2

Text-fig. 12g

Material. USNM PAL 624877, 768149.

Locality. Dakin.

Description. Seed elliptical, 2.0–2.5 mm wide, 1.2–1.8 mm tall; more than 14 parallel, latitudinal ridges with distal ends pointing towards closest pole; polar latitudinal ridges have cross ridges that decrease in frequency towards the equator.

Taxon KF3

Text-fig. 12h

Material. USNM PAL 624832.

Locality. Dakin.

Description. Seed circular 2.7 mm long, 2.2 mm wide; sculpture mostly square and rectangular reticulæ but some circular reticulæ near center.

Remarks. We compared this seed to those of *Eurya* THUNB., but the fossa of the reticulæ are more round and oriented so that the long axis of the fossa are perpendicular to the outer edge (Zhu et al. 2016).

Taxon KF4

Text-fig. 12i, j

Material. USNM PAL 625629, 768303.

Localities. Dakin and Spring.

Description. Seed subelliptical to circular 2.9–3.7 mm long, 2.5–2.8 mm wide, 0.7 mm deep; embryo curved; notch for hilar scar 1.5–1.8 mm long, 0.4 mm deep at 150° angle; depression on seed surface; reticulæ oval shaped about 26 rows tall, 22 columns wide; ovals spiral so they are oriented linearly near the center and circularly near the outside edge or ridges smooth and parallel, nine rows to center.

Remarks. The concave divot on the seed's surface and the outline of the seed bears some resemblance to the fossil genus *Rutaspermum*, which is used for seeds that are in Rutaceae. However, the sculpture seen in this fossil does not resemble that seen in any known seeds from Rutaceae. The genera *Alisma* L. and *Echinodorus* RICH. et ENGELM. ex A.Gray show all of the previously mentioned features and are more alike in sculpture (Kirkbride et al. 2000). Seeds in Alismataceae may or may not have a distinctive groove that

runs along the outer edge (Kirkbride et al. 2000). Our fossil does not. Because there is no clear match between the fossil and any modern species in *Alisma* or *Echinodorus* and there is no groove, we are hesitant to place it in Alismataceae.

Taxon KF5

Text-fig. 12k

Material. USNM PAL 624455.

Locality. Dakin.

Description. Seed subovate, 3.0 mm long, 2.4 mm wide; sculpture rectangular reticulæ.

Taxon KF6

Text-fig. 12l

Material. USNM PAL 609598.

Locality. Park.

Description. Seed circular, 1.1 mm long, 1.2 mm wide; hilar region 0.3 mm long, 0.05 mm deep; sculpture with 7 concentric wavy ridges.

Taxon KF7

Text-fig. 12m, n

Material. USNM PAL 722298, 625631.

Locality. Dakin and Spring.

Description. Seed subelliptical to elliptical with curved embryo, 1.3 mm tall, 1.1–1.2 mm wide; seven rows of circular, concentric reticulæ; hilar scar 0.5 mm wide.

Taxon KF8

Text-fig. 12o

Material. USNM PAL 625736.

Locality. Spring.

Description. Seed subobovate, 2.6 mm tall, 1.4 mm wide, hilar scar 0.4 mm, sculpture reticulate with irregularly rounded fossa; small margin surrounding the seed body 0.1 mm wide.

Remarks. We compared this seed to those in Passifloraceae and Apocynaceae. Seeds in Passifloraceae have a knob on the chalazal end and a pointed micropylar end (Martínez 2017). Our seed lacks a knob and is rounded on one end and flat antipodally. Seeds in the subfamily Asclepiadoideae (Apocynaceae) are elliptical and have a marginal lining (Del Rio et al. 2020) like our seed. This fossil was examined by photograph, so cellular detail may be preserved and reveal its true affinity through light microscopy.

Taxon KF9

Text-fig. 12p–t

Material. USNM PAL 620311, 621685, 624459, 625551, 625608, 626216.

Localities. Dakin, Park, Pisces, Spring and Tunnel Creek.

Description. Structure 2.4 mm by 2.5 mm from surface view, 1.2–1.7 mm tall and 1.0–1.2 mm wide from lateral view consisting of an apical region with three elliptical structures in surface view; U-shaped in lateral view, 0.3–0.9 mm long, 0.3–0.6 mm wide; basal circular to obovate mass 0.6–1.0 mm tall, 0.9–1.2 mm wide with apical dome 0.2–0.2 mm tall 0.2–0.3 mm wide.

Remarks. Some interpretations of these fossils are that they are flowers with three anthers, fruit with persistent epigynous perianth or full aquatic plants. More could be revealed with CT scanning.

Taxon KF10
Text-fig. 13a, b

Material. USNM PAL 729594, 624100, 624536, 622129.

Localities. Dakin and Park.

Description. Fruit ovate with truncate apex, 2.7–5.0 mm tall, 0.7–1.8 mm wide; pedicel stout, 0.5–1.1 mm long, 0.2–0.4 mm wide.

Taxon KF11
Text-fig. 13c

Material. USNM PAL 722208.

Locality. Spring.

Description. Raceme 21.4 mm long; peduncle 0.3 mm wide; pedicels 1.8–4.1 mm long, 0.1–0.2 mm wide; fruits elliptical 1.6–3.7 mm tall, 1.2–1.6 mm wide; base and apex rounded.

Taxon KF12
Text-fig. 13d, e

Material. USNM PAL 621405, 626089.

Localities. Deep Ford and Park.

Description. Structures tufts with 8–9 triangular strands 3.0–4.2 long, 0.1–0.2 mm wide at base; membrane appears around strands in USNM PAL 626089.

Taxon KF13
Text-fig. 13f

Material. USNM PAL 729855.

Locality. Park.

Description. Structure ovate, 1.5 mm tall, 0.9 mm wide at widest point; three projections at apex 0.2 mm tall; about 20 longitudinally oriented undulations on one side measuring up to 0.1 mm apart.

Taxon KF14
Text-fig. 13g

Material. USNM PAL 622021.

Locality. Disbrow Creek.

Description. Flower or fruit, pedicel 2.5 mm long, 0.1 mm wide; calyx cuneate 1.2 mm tall, 0.2 mm wide at

base of calyx; 0.7 mm at apex of calyx; three petals, tepals or wings 4.1 mm long, 0.7 mm wide; wing bases tapered, apices rounded.

Taxon KF15
Text-fig. 13h

Material. USNM PAL 622820.

Locality. Disbrow Creek.

Description. Structure obovate, feather-like 3.3 mm tall, 1.6 mm wide; 16 projections coming off main axis, 0.8–1.5 mm from axis, up to 0.1 mm wide.

Remarks. Although this structure may not be botanical, it does not appear to be a feather because it is too large to be a ramus with barbules.

Taxon KF16
Text-fig. 13i

Material. USNM PAL 722411.

Locality. Dakin.

Description. Disseminule dome shaped; 4.0 mm long, 2.1 mm tall; concentric ring forming smaller dome 3.0 mm long and 1.6 mm tall.

Remarks. Although there are some superficial resemblances to the fossil nymphaeaceous seed, *Nuphar carlquistii* DEVORE, David W. TAYLOR et PIGG, this seed is more bean-shaped than elliptical and lacks a flat pole (DeVore et al. 2015). *Nuphar* pollen is reported from Canadian exposures of the Kishenehn by Hopkins and Sweet (1976).

Taxon KF17
Text-fig. 13j

Material. USNM PAL 624059.

Locality. Dakin.

Description. Winged disseminule dome shaped, 2.8 mm long, 1.1 mm wide; seed body linear on a distal corner of the dome oriented so the long edge of the seed body is perpendicular to the flat edge of the disseminule; seed body 0.7 mm tall and 0.2 mm wide with rounded distal edges; pattern on wing is a rounded mesh.

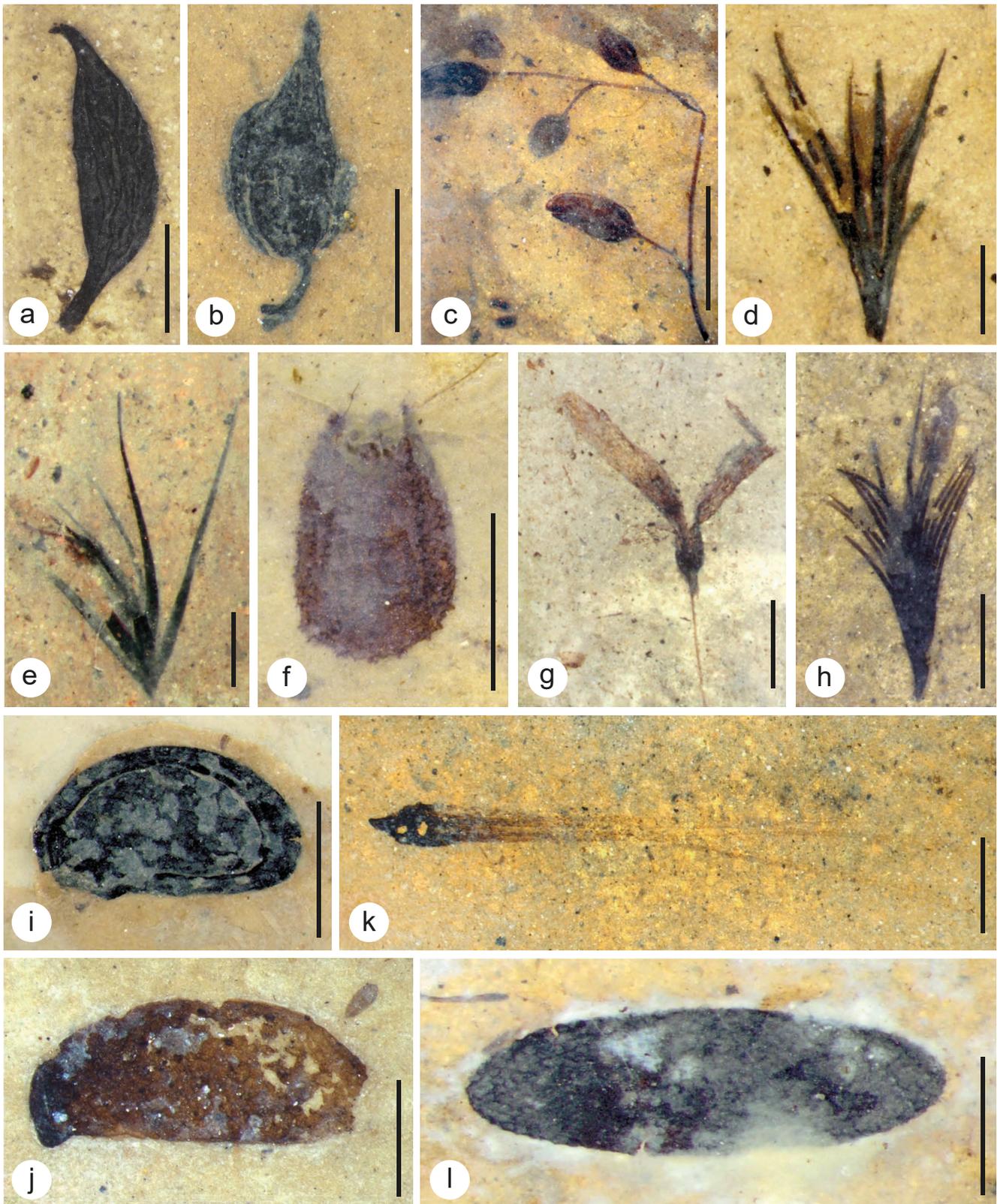
Taxon KF18
Text-fig. 13k

Material. USNM PAL 622632, 623072.

Locality. Disbrow Creek.

Description. Disseminule body 1.5 mm long, 0.9 mm wide with a flat edge attaching to hairs, the antipodal end truncated; fibrous hairs measuring 11.3 mm long.

Remarks. We compared this disseminule to fruit of *Typha* and seeds of Apocynaceae. The *Typha* fruits generally had long styles (Iowa Plants 2012), which are lacking in the fossil and the Apocynaceae seeds are tapered instead of flat on the site of hair attachment (Gabr 2014).



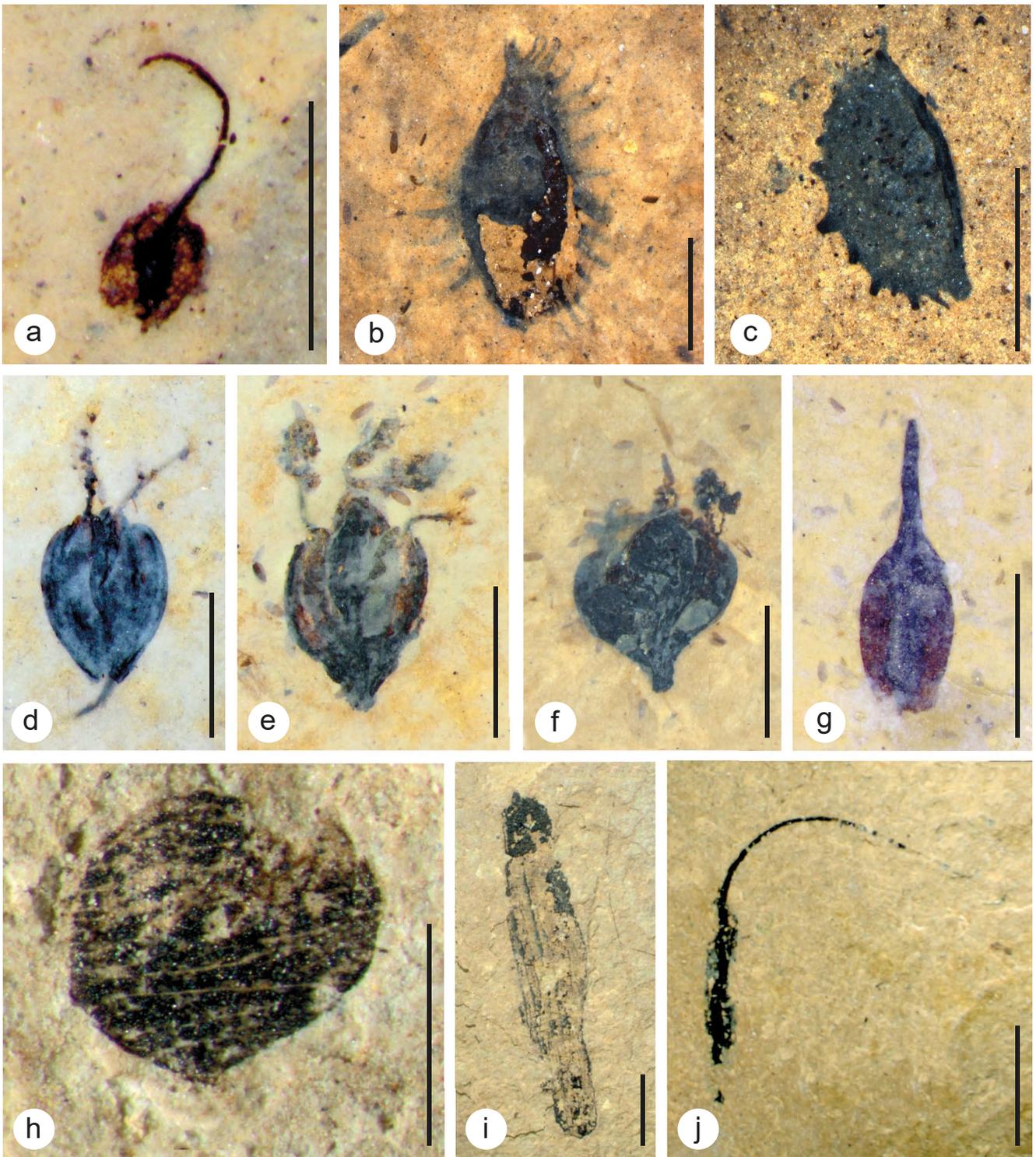
Text-fig. 13. a: USNM PAL 729594 KF10. Scale bar 1 mm. b: USNM PAL 624100 KF10. Scale bar 2 mm. c: USNM PAL 722208 KF11. Scale bar 5 mm. d: USNM PAL 626089 KF12. Scale bar 1 mm. e: USNM PAL 621405 KF12. Scale bar 1 mm. f: USNM PAL 729855 KF13. Scale bar 1 mm. g: USNM PAL 622021 KF14. Scale bar 2 mm. h: USNM PAL 622820 KF15. Scale bar 1 mm. i: USNM PAL 722411 KF16. Scale bar 2 mm. j: USNM PAL 624059 KF17. Scale bar 1 mm. k: USNM PAL 622632 KF18. Scale bar 2 mm. l: USNM PAL 626168 KF19. Scale bar 1 mm.

Taxon KF19
Text-fig. 13l

Material. USNM PAL 626168.

Locality. Deep Ford.

Description. Seed fusiform, 3.4 mm long, 1.4 mm wide; reticulate sculpture with hexagonal reticulæ 0.1 mm across.



Text-fig.14. a: USNM PAL 621654 KF20. Scale bar 1mm. b: USNM PAL 625887 KF21. Scale bar 2mm. c: USNM PAL 625733 KF22. Scale bar 2mm. d: USNM PAL 712973 KF23. Scale bar 2mm. e: USNM PAL 624779 KF24. Scale bar 2mm. f: USNM PAL 622683 KF25. Scale bar 2mm. g: USNM PAL 624973 KF26. Scale bar 2mm. h: USNM PAL KF27. Scale bar 1mm. h: USNM PAL 619968 KF28. Scale bar 5mm. j: USNM PAL 619979 KF29. Scale bar 5mm.

Remarks. Unlike the other reticulate seeds from the Kishenehn, this seed is fusiform instead of circular.

Taxon KF20
Text-fig. 14a

Material. USNM PAL 621654.

Locality. Tunnel Creek.

Description. Disseminule elliptical body with dispersal hair, 1.4 mm long; main body 0.4 mm long, 0.4 mm wide; dispersal hair 1.0 mm long; seed body 0.3 mm long, 0.2 mm wide.

Taxon KF21
Text-fig. 14b

Material. USNM PAL 625887.

Locality. Brown's Hole.

Description. Disseminule obovoid; main body 5.1 mm long, 2.0 mm wide; more than 21 hook-like projections, apices pointed basally 0.4–0.8 mm long 0.1–0.2 mm at base.

Remarks. This specimen, with many barbs, has a superficial resemblance to the Cynoglossoideae of the Boraginaceae. However, Cynoglossoideae fruits have the widest part of their nutlets at their bases instead of near the center (Guo 1998, Kong and Hong 2016). Other possible affinities include the genera *Torilis* ADANS., *Daucus* L. and *Lecokia* DC. in the Apiaceae and *Xanthium* L. in the Asteraceae. The fossil has no obvious suture, which would be indicative of *Torilis*, and is larger than most *Xanthium* fruits (Guo 1998). Regardless of its taxonomic affinities, the barbs on the fruit indicate an epizoochorous mode of dispersal.

Taxon KF22
Text-fig. 14c

Material. USNM PAL 625733.

Locality. Spring.

Description. Schizocarp with flat axial margin and curved distal margin 2.8 mm long and 1.3 mm wide; axial margin with line of dehiscence 0.2 mm wide; projections on distal surface up to 0.3 mm long, 0.1–0.2 mm wide at the base; basal and apical ends of fruit indiscernible, one polar end possessing stout cylinder 0.2 mm long, 0.2 mm wide and the antipolar end possessing projection 0.3 mm long, 0.1 mm wide.

Remarks. Possible affinities for this fossil are Boraginaceae (Kong and Hong 2016) and Apiales because it is a semicircular schizocarp with projections.

Taxon KF23
Text-fig. 14d

Material. USNM PAL 712973.

Locality. Dakin.

Description. Flower with pentamerous perianth; longitudinally striated, 2.2 mm tall, 0.6 mm wide; perianth apices rounded; two staminal tubes 1.3–1.5 mm tall, up to 0.1 mm wide; anthers round up to 0.1 mm in diameter; 4–14 anthers on staminal tube.

Taxon KF24
Text-fig. 14e

Material. USNM PAL 624779.

Locality. Dakin.

Description. Flower with three visible perianth parts 2.1 mm tall with rounded apices, 1.0 mm wide; four anthers visible; filaments exerted 0.6–0.7 mm above perianth, 0.1 mm wide; anther attachment mode unknown; anthers elliptical 0.8 mm long, 0.5 mm wide.

Taxon KF25
Text-fig. 14f

Material. USNM PAL 622683.

Locality. Disbrow Creek.

Description. Flower globose, 6.5 mm long, 3.0 mm wide; pedicel 3.3 mm long, 0.3 mm wide; three perianth units present with rounded apices, 2.0–2.7 mm tall, 1.0–1.4 mm wide; at least three stamens, filaments exerted 0.3 mm above perianth, 0.1 mm wide; anthers with versatile attachment, 0.4 mm long, 0.2 mm wide; single pistil 0.2–0.6 mm above perianth 0.3 mm wide with a slanted single stigma.

Taxon KF26
Text-fig. 14g

Material. USNM PAL 624973.

Locality. Spring.

Description. Disseminule with obovate body and linear distal end, 3.5 mm long, 1.1 mm wide; main body 1.9 mm long; distal end 1.6 mm long; darker portion in center measuring 0.5 mm wide.

Taxon KF27
Text-fig. 14h

Material. USNM PAL 619970.

Locality. Park.

Description. Seed subelliptical 1.3 mm tall, 1.5 mm wide; 10 straight grooves, mostly parallel but at slight angles; rim outlining seed.

Remarks. The fossil differs from "KF2" by being slightly smaller, having a rim, fewer grooves and the grooves being at slight angles.

Taxon KF28
Text-fig. 14i

Material. USNM PAL 619968.

Locality. Park.

Description. Structure fusiform 24.0 mm long, 4.7 mm wide; rounded poles; eight large longitudinal ridges with smaller striations in between.

Taxon KF29
Text-fig. 14j

Material. USNM PAL 619979.

Locality. Park.

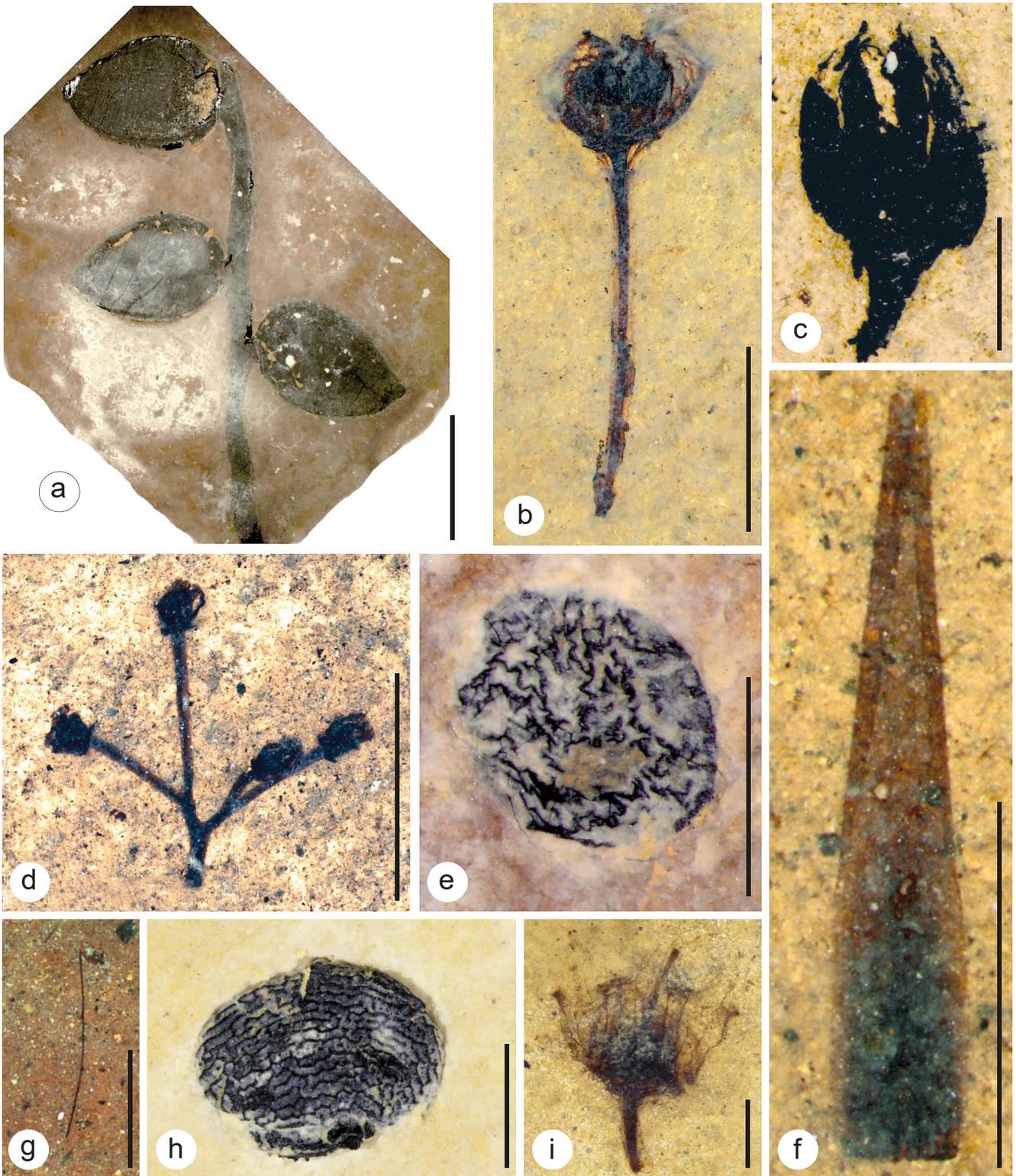
Description. Disseminule with dispersal hair; disseminule body fusiform 8.3 mm long, 1.0 mm wide; longitudinal ribs present; dispersal hair 12.3 mm long.

Remarks. This could be interpreted as Poaceae with a seed body and dispersal hair (Guo 1998).

Taxon KF30
Text-fig. 15a

Material. USNM PAL 625749.

Locality. Spring.



Text-fig. 15. a: USNM PAL 625749 KF30. Scale bar 1 cm. b: USNM PAL 621569 KF31. Scale bar 5 mm. c: USNM PAL 625828 KF32. Scale bar 2 mm. d: USNM PAL 625723 KF33. Scale bar 5 mm. e: USNM PAL 712972 KF34. Scale bar 2 mm. f: USNM PAL 621401 KF35. Scale bar 2 mm. g: USNM PAL 625396 KF36. Scale bar 2 mm. h: USNM PAL 768133 KF37. Scale bar 1 mm. i: USNM PAL 768114 KF38 flower. Scale bar 2 mm.

Description. Raceme 4.0 cm long, 1.6 mm wide with three woody, ovate, capsular fruit. Fruit borne perpendicular to the peduncle on a stout pedicel 0.5 mm long and 2.0 mm wide or sessile; fruit 1.2 cm long, 0.8–0.9 cm wide at widest, symmetrical to asymmetrical with distal side of fruit curving to apex before proximal side.

Taxon KF31

Text-fig. 15b

Material. USNM PAL 621569.

Locality. Park.

Description. Capsular fruit 13.3 mm long (with pedicel); pedicel 10.1 mm long; 0.7 mm wide and widens to

1.8 mm at apex; perianth persistent (2.2 mm wide); capsule oblate spheroid 4.4 mm wide, center vertical axis of fruit is shorter (2.4 mm tall) than medial vertical axes (3.2 mm tall) forming triangular valve apices.

Taxon KF32
Text-fig. 15c

Material. USNM PAL 625828.

Locality. Stanton Creek.

Description. Pedicel stout, 1.6 mm long, 0.4 mm wide at base and 1.4 mm wide at apex; calyx 3.3 mm long and 2.7 mm wide; 4 sepals in view 0.9–1.8 mm long and 0.4–0.6 mm wide

Taxon KF33
Text-fig. 15d

Material. USNM PAL 625723.

Locality. Spring.

Description. Compound umbel 6.9 mm tall; peduncle 1.2 mm tall, 0.4 mm wide; peduncle 0.4 mm long, 0.2–0.3 mm wide; pedicels 1.6–3.4 mm long, 0.1–0.3 mm wide increasing in diameter distally; umbel bifurcating twice to form two sets of two flowers/fruit; perianth present 0.6–0.8 mm wide, flowers/fruit hexagonal in lateral view, 0.8–1.1 mm tall 0.6–1.1 mm wide at widest point.

Taxon KF34
Text-fig. 15e

Material. USNM PAL 712972.

Locality. Disbrow Creek.

Description. Seed subelliptical 2.7 mm long, 2.1 mm wide; reticulated sculpture with wrinkled muri forming irregularly shaped fossa.

Remarks. The most distinguishing feature of this seed are the wrinkled muri.

Taxon KF35
Text-fig. 15f

Material. USNM PAL 621401, 622342, 624791.

Localities. Dakin, Disbrow Creek and Park.

Description. Structure thin, triangular, 2.7–4.5 mm long, 0.4–0.7 mm wide at base; dark blotch at base climbing 1.4–2.0 mm tall dissipating apically; lateral edges curled inwards.

Taxon KF36
Text-fig. 15g

Material. USNM PAL 625396.

Locality. Spring.

Description. Pedicel 3.2 mm long; obovate epigynous calyx attached perpendicularly to apex of pedicel; calyx 0.4 mm tall and 0.2 mm wide; calyx base acutely rounded, and apex tapers then flares outward to expose calyx parts.

Taxon KF37
Text-fig. 15h

Material. USNM PAL 768133.

Locality. Dakin.

Description. Seed elliptical, 1.6 mm long, 2.0 mm wide; sculpture 16 horizontally parallel wavy ridges.

Taxon KF38
Text-fig. 15i

Material. USNM PAL 768114.

Locality. Dakin.

Description. Flower 6.5 mm tall, 5.3 mm wide; pedicel 2.0 mm tall, 0.5 mm wide at base and 0.6 mm wide at apex; disc 3.3 mm wide; style 2.2 mm tall, 0.2 mm wide; bracts 5.0 mm long; bract apex forms 59° angle; longitudinal bract veins prominent connected by thinner perpendicular veins; sinus between bracts 40 % of bract length.

Remarks. We compared this fossil with laterally compressed *Florissantia* KNOWLT. fossils but found our fossil's floral cross venation was weaker.

Taxon KF39
Text-fig. 16a

Material. USNM PAL 620017.

Locality. Park.

Description. Aggregate of achenes on pedicel 1.7 cm long, 0.2 cm wide, fruit rectangular in lateral view, fruit 1.3 cm tall, 2.3 cm wide, base flat, apex, and sides with seed ridges.

Remarks. *Alisma* L. (Alismataceae VENT.) fruits are an aggregate of achenes with a flat base and the achenes may have a groove on the edge surrounding the hilar scar (Native Plant Trust 2023, TMI 2022). This fruit is larger than the largest in North America today (*Alisma lanceolatum* WITH.), which measures up to 8 mm across (Haynes and Hellquist 2020). Although *Malva* L. (Malvaceae JUSS.) has similar looking fruit, we would expect to see its persistent sepals (Hill 2022).

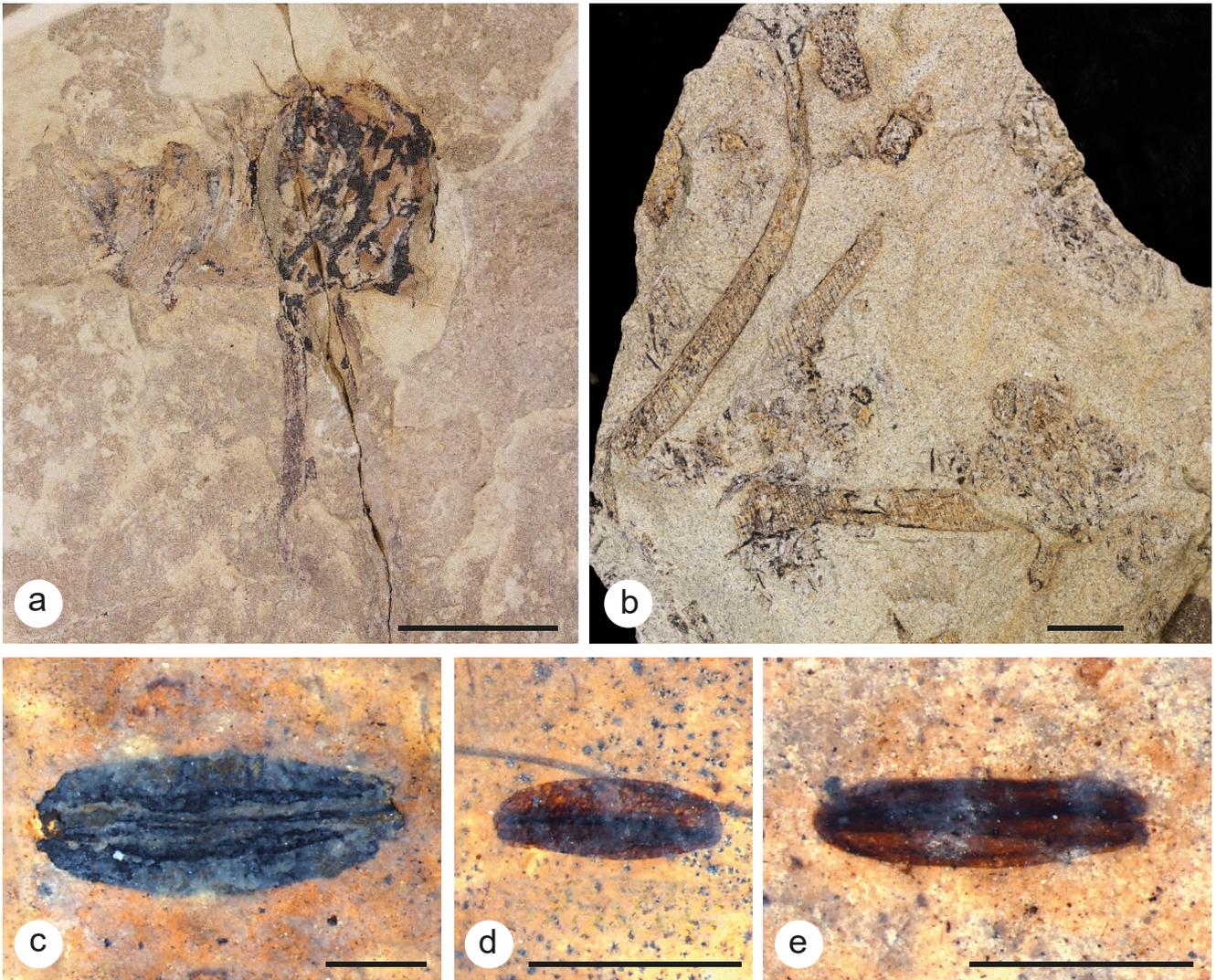
Taxon KF40
Text-fig. 16b

Material. USNM PAL 776569.

Locality. Disbrow Creek.

Description. Follicles linear, at least 6.2 cm long, 0.5–0.6 cm wide; many septa or fibers running at an angle slightly past perpendicular to the fruit wall.

Remarks. Follicles are present in both the Cercidiphyllaceae and the Catalpae though neither have septa. These fruits are larger than any known cercidiphyllaceous fruit, establishing some doubt as to their true affinity (Golovneva and Zolina 2018, Kajita et al. 2021).



Text-fig. 16. a: USNM PAL 620017 KF39. Scale bar 1 cm. b: USNM PAL 776569 KF40. Scale bar 1 cm. c: USNM PAL 621212 KF41. Scale bar 2 mm. d: USNM PAL 624361 KF42. Scale bar 2 mm. e: USNM PAL 625642 KF43. Scale bar 2 mm.

Taxon KF41

Text-fig. 16c

Material. USNM PAL 621212.

Locality. Park.

Description. Disseminule fusiform, 6.9 mm long, 2.8 mm wide; with three parallel longitudinal lines.

Remarks. It is hard to discern if the three lines represent ridges, grooves or a combination of them. If it represents a central groove, the full disseminule would be larger than seeds found in Hydrocharitaceae or *Plantago* but in the size range of grasses (Guo 1998, Kirkbride et al. 2000, Canadian Food Inspection Agency 2017).

Taxon KF42

Text-fig. 16d

Material. USNM PAL 624361.

Locality. Dakin.

Description. Seed fusiform 2.2 mm long, 0.8 mm wide, rounded edges, sulcus running from pole to pole, dots present on surface.

Remarks. The dots on this seed may be resin cells or divots. The seed does have similar morphology and size to seeds found in Hydrocharitaceae and *Plantago* (Kirkbride et al. 2000, Canadian Food Inspection Agency 2017).

Taxon KF43

Text-fig. 16e

Material. USNM PAL 625642.

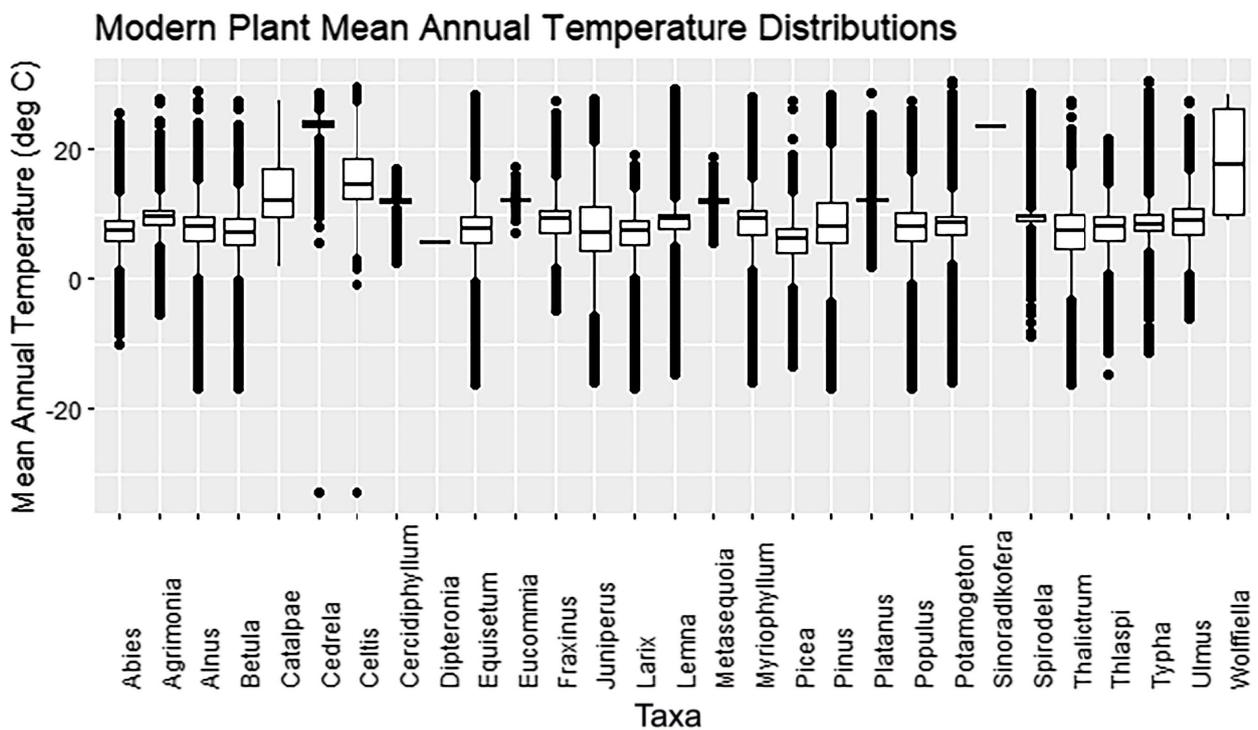
Locality. Dakin.

Description. Structure fusiform, 3.0 mm long, 0.8 mm wide; sulcus running from pole to pole, one pole rounded and opposite pole with indent; circular to elliptical cell pattern.

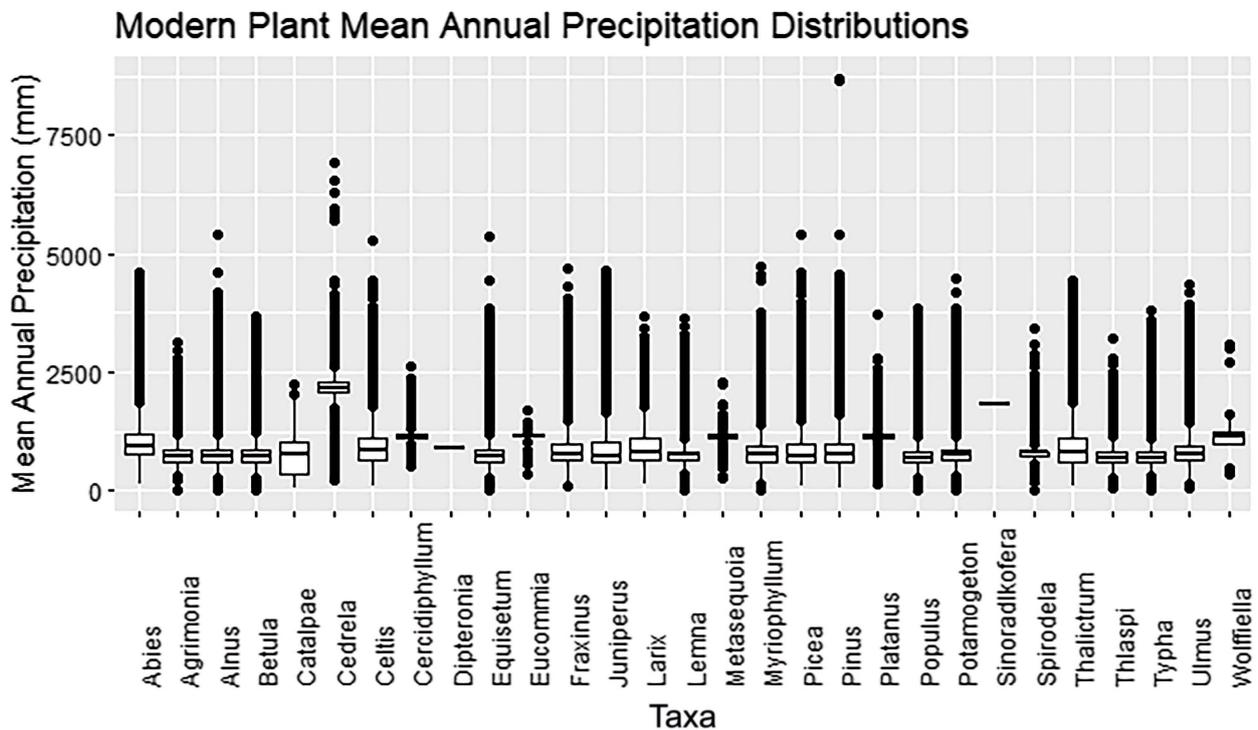
Remarks. This structure is longer than KF42 but roughly the same width. It differs by having a distinctive cellular pattern instead of dots. Possible affinities include *Plantago* and grasses (Guo 1998, Canadian Food Inspection Agency 2017).

Paleoclimate

Results from the Bioclimatic and mutual climate range analyses (BA/MCRT) following the methods of Kotthoff et al.



Text-fig. 17. Modern mean annual temperature ranges of the Kishenehn taxa. Note that *Sinoradlkofera* is indicated by its synonym, *Boni dendron*, in GBIF (2023). Thick lines are only apparent and are actually overlapping outlier points. Points below -20°C were assumed to be incorrect and removed from consideration.



Text-fig. 18. Modern mean annual precipitation ranges of the Kishenehn taxa. Note that *Sinoradlkofera* is treated as *Boni dendron* in GBIF (2023). Thick lines are only apparent and are actually overlapping outlier points.

(2014) are summarized in Tab. 3. Mean annual temperature is estimated to have been between 8.91 and 12.10°C and mean annual precipitation is estimated to have been between 945 and $1,204$ mm per year. The warmest months had more precipitation than the coldest months. The minimum temperature of the

coldest month was between -5.00 and -0.50°C and the average temperature of the three coldest months was -1.4°C . Text-fig. 17 displays the mean annual temperature ranges for the Kishenehn taxa and Text-fig. 18 displays the mean annual precipitation ranges for the Kishenehn taxa. *Dipteronia* and

Table 3. BA/MCRT results. Mean Annual Temperature (MAT), Maximum Temperature of Warmest Month (MaxTWarm), Minimum Temperature of Coldest Month (MinTCold), Mean Temperature of Wettest Quarter (T3Wet), Mean Temperature of Driest Quarter (T3Dry), Mean Temperature of Warmest Quarter (T3Warm), Mean Temperature of Coldest Quarter (T3Cold), Annual Precipitation (MAP), Precipitation of Wettest Month (MaxPWet), Precipitation of Driest Month (MinPDry), Precipitation of Wettest Quarter (P3Wet), Precipitation of Driest Quarter (P3Dry), Precipitation of Warmest Quarter (P3Warm) and Precipitation of Coldest Quarter (P3Cold). All temperatures are in degrees Celsius and precipitation is in millimeters.

MAT	MaxT-Warm	MinT-Cold	T3Wet	T3Dry	T3Warm	T3Cold	MAP	Max-PWet	MinPDry	P3Wet	P3Dry	P3Warm	P3Cold
8.91–12.10	23.80–28.1	–5.00–0.50	10.57–17.2	4.52–8.28	16.77–21.00	–1.4–1.4	945–1204	97–123	28–74	273–344	105–209	196–302	111–277

Boniodendron (Sinoradlkofera) were removed because of too few occurrences.

Discussion

Forest Structure

The presence of scansorial animals and certain insects (e.g., *Cyttaromyia lynnae*) has led several authors to believe that a dense forest bordered the lake (Dawson and Constenius 2018, Greenwalt et al. 2019, Pierce and Constenius 2014). Although cuticular studies have not been conducted on the leaves, the presence of needle-leaved *Juniperus* could be interpreted as coming from a low-light environment or dense canopy. These leaves may have also been from inside branches or from a younger tree but as of now they seem to support the dense forest hypothesis.

Plants of note

In this paper we recognize the oldest macrofossils of *Lemna*, *Chenopodium* and *Thlaspi* and potentially *Thalictrum* and *Myriophyllum* as well as the first reported fossils of *Wolffiella* and *Agrimonia*. We also recognize two new genera and species of uncertain affinity: *Pteroheterochrosperma horseflyensis* and *Quadrastubulaflora kishenehnensis*.

Pollination syndromes

Here, we explore possible relationships between known plants and pollinators from Kishenehn based on modern pollinator-plant relationships. Out of the 50 species that represent pollen-producing (seed) plants for which we have some confidence of their affinities (Tab. 4) 68 % (34 species) are pollinated primarily by wind, 8 % (4 species) by water and 20 % by (or possibly by) insects (10 species). The orders of insects with pollinators found at Kishenehn include Lepidoptera, Coleoptera, Hymenoptera and Diptera (Greenwalt et al. 2015). Of the dipterans known from the Kishenehn, the genera *Bibiodes* COQUILLET (Scudder and Cannings 2006), *Helius* LEPELETIER et SERVILLE (Kania-Kłosok 2021), *Eoanomala* GREENWALT et EVENHUIS (Greenwalt et al. 2015), *Drapetis* MEIGEN (Ollerton et al. 2009) and *Lonchoptera* MEIGEN (Orford et al. 2016) are known to have modern pollinators or come from a pollinating family (Greenwalt et al. 2019). The extinct genus *Eosciarites* RASNITSYN may have also been a pollinator since extant members of the family Sciaridae are pollinators (Koschnitzke 2018, Greenwalt et al. 2019). Despite a number of potential pollinators and

several animal-pollinated plants, our calculation of 29.4 % zoophily for the Kishenehn site falls below the global modern percentage of animal-pollinated angiosperms (87.5 %) (Ollerton et al. 2011). The percentage of animal-pollinated plants varies with climate from 78 % in temperate to 94 % in tropical climates (Ollerton et al. 2011). We are not saying that Kishenehn and modern rates are different, rather that there is an appearance of a difference. It has yet to be assessed if this low percentage in animal pollination is a consequence of taphonomy (underrepresentation of herbaceous taxa) or perhaps reflects the presence of extinct taxa, for which pollination syndromes remain poorly unknown. Macroflora studies rarely look at the relationship with pollinators and perhaps these data can help change that.

Dispersal

The Kishenehn flora is dominated by wind-dispersed disseminules (72.5 %, 37 species). This is followed by epizoochory (9.8 %, 5 species), hydrochory (5.9 %, 3 species), gravity/non-specialized (3.9 %, 2 species), either wind or gravity/non-specialized (2 %, 1 species) and endozoochory (2 %, 1 species) (Tab. 4). The high relative abundance of wind dispersed taxa is likely due to disseminules falling or wind-blown into the lake randomly and their flat orientation. Among the animal-dispersed disseminules, potential agents for dispersal of *Rutaspermum* may have included *Stockia* GAZIN, *Tarkadectes* MCKENNA (Order Primates), the ischyromyids (Order Rodenta), *Hyopsodus* LEIDY (Order Condylarthra), *Epihippus* MARSH, the brontotheriids, *Helaletes*, *Amyrnodon* MARSH (Order Perissodactyla) and *Antiacodon* MARSH (Order Artiodactyla) because their molars are larger than the fruit (Dawson and Constenius 2018). By contrast, *Ectypodus* MATTHEW et GRANGER (Order Multituberculata), *Herpetotherium* COPE, *Peradectes* MATTHEW et GRANGER (Order Marsupialia), *Troglemur* MATTHEW, *Uintasorex* MATTHEW (Order Primates), the leporid (Order Lagomorpha), *Microparamys* WOOD, *Pauromys* WOOD, the eomyid (Order Rodenta) all have teeth smaller than the *Rutaspermum* (Dawson and Constenius 2018). Of course, teasing apart predation and dispersal can be hard in the fossil record. No aquatic bird fossils (the likely dispersers of the lemnoids) have been found at Kishenehn. The lemnoids and other epizoochorous disseminules may also have been dispersed by mammals.

Comparison with the pollen

The genera *Metasequoia*, *Pinus*, *Picea*, *Typha*, *Alnus*, *Betula* and *Ulmus* reported as palynomorphs (Hopkins and

Table 4. Summary of plants identifiable to a taxonomic group from the Kishenehn Formation in Montana. fl – flower, fr – fruit, l – leaf, p – whole plant, se – seed, st – stem. Note that listed pollinators and dispersal mechanisms are only the dominant entities or modes since many plant taxa do not have an exclusive pollinator or disperser.

Taxa	Organ	Growth habit	Pollinator	Dispersal mechanism
<i>Equisetum</i>	l, st	Herbaceous	N/A	Anemochory
<i>Juniperus</i>	l	Tree	Wind	Anemochory
<i>Metasequoia</i>	l, se	Tree	Wind	Anemochory
Cupressoideae 1	l	Tree	Wind	Anemochory
Cupressoideae 2	l	Tree	Wind	Anemochory
Cupressoideae 3	l	Tree	Wind	Anemochory
Cupressoideae 4	l	Tree	Wind	Anemochory
<i>Abies</i>	se	Tree	Wind	Anemochory
<i>Larix</i>	se, c	Tree	Wind	Anemochory
<i>Picea</i> 1	se	Tree	Wind	Anemochory
<i>Picea</i> 2	se	Tree	Wind	Anemochory
<i>Pinus</i> 1	se	Tree	Wind	Anemochory
<i>Pinus</i> 2	se	Tree	Wind	Anemochory
<i>Pinus</i> 3	se	Tree	Wind	Anemochory
<i>Pinus</i> 4	se	Tree	Wind	Anemochory
<i>Pinus</i> 5	se	Tree	Wind	Anemochory
<i>Pinus</i> 6	se	Tree	Wind	Anemochory
<i>Spirodela</i>	p	Floating aquatic	Water	Epizoochory (Bird)
<i>Lemna</i>	p	Floating aquatic	Water	Epizoochory (Bird)
<i>Wolffiella</i>	p	Floating aquatic	Water	Epizoochory (Bird)
<i>Potamogeton</i>	fr, st, l	Standing aquatic	Wind	Hydrochory
<i>Typha</i>	fr	Standing aquatic	Wind	Anemochory
<i>Ceratophyllum</i>	fr	Submerged aquatic	Water	Hydrochory
<i>Thalictrum</i>	fr	Herbaceous	Wind or Insect	Anemochory
<i>Platanus</i>	l, fr	Tree	Wind	Anemochory or Gravity
<i>Myriophyllum</i>	fr	Submerged and standing aquatic	Insect	Hydrochory
<i>Jenkinsella</i>	l, fr, se	Tree	Wind	Anemochory
<i>Populus</i>	fr	Tree	Wind	Anemochory
Legume 1	fr	Unknown	Unknown	Unknown
Legume 2	fr	Unknown	Unknown	Unknown
<i>Agrimonia</i>	fr	Herbaceous	Bee	Epizoochory (Mammal)
<i>Ulmus</i>	l, fr	Tree	Wind	Anemochory
<i>Palaeocarya</i>	fr	Tree	Wind	Anemochory
Betuloideae	se	Tree	Wind	Anemochory
<i>Alnus</i> 1	se	Tree	Wind	Anemochory
<i>Alnus</i> 2	se	Tree	Wind	Anemochory
<i>Betula</i>	se	Tree	Wind	Anemochory
<i>Dipteronia</i>	fr	Tree	Wind	Anemochory
<i>Boniodendron</i>	fr, se	Tree	Wind	Anemochory
<i>Ailanthus</i>	fr	Tree	Bee	Anemochory
<i>Cedrela</i>	se	Tree	Moth	Anemochory
<i>Rutaspermum</i>	se	Tree	Bee	Endozoochory (Bird or Mammal)
<i>Thlaspi</i>	fr	Herbaceous	Wind	Anemochory
KF38	fl	Unknown	Bee	Anemochory
<i>Deviacer</i>	fr	Tree	Insect	Anemochory
<i>Chenopodium</i> 1	se	Herbaceous	Wind	Gravity
<i>Chenopodium</i> 2	se	Herbaceous	Wind	Gravity
<i>Eucommia</i>	fr	Tree	Wind	Anemochory
<i>Fraxinus</i>	fr	Tree	Wind	Anemochory
Catalpeae	se	Tree	Bee	Anemochory
Apiales	fr	Unknown	Insect	Epizoochory (Bird or Mammal)

Table 5. Mean annual temperature comparison of selected Eocene western North American sites.

Locality/Flora	Age	MAT (°C)	Depositional environment	Source
Puget Group, WA (n = 4)	Early and middle Eocene?	23.20–24.44 ^a 17.74–19.69 ^b	?	Spicer 2011–2023
East Birch Creek, OR	Early Eocene	23.4 ± 4.3 ^a	Fluvial?	Jijina et al. 2019
Big Horn Basin, WY (n = 4)	Early Eocene	16–22	Floodplain	Currano et al. 2010
John Day Gulch, OR	Middle Eocene	19.05 ± 2.35 ^a 17.60 ± 1.99 ^b	Lacustrine	Myers 1998
White Cliffs (Jr.), OR	Middle Eocene	17.05 ± 3.06 ^a 17.02 ± 1.99 ^b	Lacustrine	Myers 1998
Arbuckle Mountain, OR	Middle Eocene	16.4 ± 4.2 ^a	Floodplain	Jijina et al. 2019
Slide Member of Chuckanut, WA (n = 3)	Early Eocene	19.8–23.6 ^a 15.3–16 ^b	Meandering river	Breedlovestrout 2011
Nut Beds, OR	Early or middle Eocene	14.3–15.1 ^a 17.0 ^b 14.7–18.8 ^c 14.6–18.8 ^d 12.5–15.4 ^e	Lacustrine delta	Greenwood 1992, Wolfe 1997, Herman and Spicer 1996, Wing and Greenwood 1993, Gregory 1994, Wheeler and Manchester 2002
Falkland, BC	Early Eocene	6.8 ± 2.0 ^a 11.9 ± 2.0 ^b	Lacustrine	Smith et al. 2009
Quilchena, BC	Early Eocene	14.6 ± 4.8 – 16.2 ± 2.0 ^a 13.3 ± 2.1 ^b	Upland lacustrine	Mathewes et al. 2016
Bonanza, UT	Middle Eocene	15	Lacustrine	Royer et al. 2007
Bellingham Bay Member of Chuckanut, WA (n = 5)	Early Eocene	18.3–22.6 ^a 17.1–18.8 ^b	Meandering river with floodplain	Breedlovestrout 2011
Padden Member of Chuckanut, WA (n = 2)	Early to middle Eocene?	13.4–15.7 ^a 13–15.3 ^b	Braided and coarseload meandering river	Breedlovestrout 2011
Maple Falls Member, Chuckanut, WA	Early to middle Eocene?	14.6 ^a 12.3 ^b	Alluvial fan and plain	Breedlovestrout 2011
West Branch Creek, OR	Middle Eocene	14.53 ± 3.10 ^a 13.12 ± 1.99 ^b	Lacustrine	Myers 1998
Florissant, CO	Late Eocene	11–14	Upland lacustrine	Allen et al. 2020
McAbee, BC	Early Eocene	8–14	Upland lacustrine	Lowe et al. 2018
Republic, WA	Early Eocene	~9	Upland lacustrine	Royer et al. 2007

Sweet 1976) are also represented among the megafossils recognized herein. The grains described as *Acer* may be *Dipteronia* due to their similarities and those of *Engelhardia* may belong to the *Palaeocarya* due to their relatedness (Hopkins and Sweet 1976). The remainder have either yet to be found, are found too far away from the depositional basin or do not occur in the Montana localities.

Paleoclimate

We recognize that the methods derived from the coexistence approach (CoA), such as BA/MCRT, have been seriously challenged (Grimm et al. 2016). Inherent errors include not having a nearest living relative, different climatic tolerances between the fossil and nearest living relative, the complete tolerance of the nearest living relative is not exploited in its realized niche and unreliable climatic data. We still find CoA and its derivations useful to provide an estimate, especially when there are low numbers of leaf morphotypes, which negatively impacts the precision of the estimate (Povey et al. 1994, Spicer et al. 2009).

With the exception of *Dipteronia* and *Boniodendron* it would appear that all of the taxa can coexist within the estimated climatic variables. The reason for *Dipteronia* and

Boniodendron non-overlapping in climatic tolerances may have less to do with their physiology and more to do with the limited occurrence data on extant populations.

The molluscan record for the Kishenehn beds shows there were three communities, by using modern analogues: a tropical group that lives in the Caribbean, Central and South America; a subtropical/semi-arid group that lives in the north coast of the Gulf of Mexico to southern California and the Baja Peninsula and a warm-humid group transported from the bordering mountains to the east that were deposited in the delta and lake (Pierce and Constenius 2014). It is probable that multiple communities existed with more warm-tolerant species like *Boniodendron*, *Dipteronia*, *Cedrela*, *Platanus* and *Macginitiea* at the base of the basin and more cold-tolerant species such as *Larix* up on the mountain (see Pierce and Constenius 2014 for explanation of the topography). Likewise, the lake may cause a black-body effect, generating warmer temperatures around the basin. We note that although trees such as *Abies*, *Alnus*, *Betula* and *Picea* are popularly thought of as cold-tolerant, they also exist in tropical regions where MAT is above 21 °C (Text-fig. 16).

Another problem mentioned in Grimm et al. (2016) is that an extant genus may not have the same climatic tolerances

today as its extinct representatives. This consideration may have implications for *Cercidiphyllum* being considered a “nearest modern relative” for *Jenkinsella*. It can also be a problem for taxa that were once widespread and diverse that have suffered extinction over a large portion of their original range, e.g., *Dipteronia*, *Eucommia*.

We note the absence of certain tropical indicator species such as palms and cycads (in the macro- and microfossil record) and apparently low or absent liana diversity. So far, no lianas have been identified from the Kishenehn. For example, along with Arecaceae, families with lianas that are common in other warm Eocene floras such as Menispermaceae, Vitaceae, and Icacinaceae are apparently missing (Manchester 1994, Wilde and Frankenhäuser 1998, Reid and Chandler 1933). There are, however, crocodylian teeth (Dawson and Constenius 2018), which are an indicator of low frost, and recently, insects implying a “subtropical” climate have been identified (Jepson and Makarkin 2023). Whereas our MAT estimates are not particularly warm (8.91–12.10 °C), our lowest temperature for the coldest month is between –5 and –0.5 °C and average temperature for the three coldest months is –1.4 °C. Looking at coldness is important for determining biogeographical ranges because freezing water can lyse cells or inhibit other cellular activity (Reichgelt et al. 2018). It would also appear that the Kishenehn experienced low seasonality which fits the global condition at the time (Smith et al. 2012).

An estimate of 8.91–12.10 °C puts Kishenehn on par with a number of other fossil localities (Table 5). The earlier Falkland, Quilchena, McAbee and Republic floras were mesic forests near upland lakes with MAT estimates ranging from 6.8–11.9 °C, 11.1–19.4 °C, 8–14 °C and 9 °C, respectively (Smith et al. 2009, Mathewes et al. 2016, Allen et al. 2020). Early Eocene floodplain sediments of the Big Horn Basin of Wyoming ranged from 16–22 °C (Allen et al. 2020). Bonanza, a Green River Formation lacustrine deposit in northeastern Utah was estimated to be 15 °C (Allen et al. 2020). MAT estimates for the deltaic and fluvial deposits of western Washington’s Paleocene to late Eocene Chuckanut Formation range from 12–22.6 °C (Mustoe et al. 2007, Breedlovestrout 2011). The coeval Clarno Nut Beds and Arbuckle Mountain floras of central and eastern Oregon are estimated to have been 14.7–18.8 °C and 16.4 ± 4.2 °C, respectively (Wiemann et al. 1998, Wheeler and Manchester 2002, Jijina et al. 2019). Lastly, temperatures from the late Eocene chaparral lake deposits of Florissant, Colorado are estimated to have been 11–14 °C (Allen et al. 2020). Given that the Kishenehn is younger than the floras with temperature estimates to the west and north and that the Kishenehn is further north and inland of the coeval floras (Clarno floras, Maple Falls Member of the Chuckanut, Arbuckle Mountain) that have been analyzed for MAT, estimates between 8.91 and 12.10 °C seem reasonable. Cooler temperatures compared to those west is likely due to a combination of continentality and mountains and plateaus to the west.

Leaf physiognomic methods such as leaf margin analysis (LMA) and Climate Leaf Analysis Multivariate Program (2011–2023) are additional ways to estimate paleoclimate. However, these methods require a minimum of 20 woody dicot morphospecies (Wolfe 1971, Spicer et al. 2009, Peppe et al. 2018) to give results with reliable precision. Although

a full study on the leaves of Kishenehn has not been conducted, a preliminary survey showed LMA or CLAMP analysis results would have to be viewed with caution. Only two leaves were observed with entire margins, a small proportion, which greatly reduces the probability that the Kishenehn basin had a high MAT. As with all paleoclimate estimations, examining a flora may combine plants that lived decades to millennia apart and may not be from the same climatic regime (Grimm and Potts 2016).

Biogeography

The Kishenehn flora represents the northernmost middle Eocene locality in the United States Rocky Mountain region. Lutetian-aged (47.8–41.2 Ma) outcrops in northwestern North America include the Thunder Mountain flora in Idaho (Axelrod 1998, Erwin and Schorn 2005), the Higgins Mountain (Mt. Higgins), Sperry Creek and Grade Creek Units of the Chuckanut Formation in western Washington (Breedlovestrout 2011), the Clarno Formation of central Oregon (Manchester 1994) and the Princeton Chert from the Allenby Formation of the Okanagan Mountains in British Columbia (though conflicting dates put this flora at the end of the Ypresian and the Lutetian dates were never officially published) (Pigg and DeVore 2016). Somewhat older floras in northern and western North America include the early Eocene to early middle Eocene Green River Formation to the south in Wyoming, Utah and Colorado (Brown 1929, Wing 1987); and in western Canada including the McAbee (53–51 Ma) (Lowe et al. 2018), Thomas Ranch 49 ± 4 Ma (Dillhoff et al. 2013), Quilchena (51.5 ± 0.4 Ma) (Mathewes et al. 2016), Falkland (50.61 ± 0.61) (Smith et al. 2012) and Horsefly floras (Penhallow 1908) of the Okanagan Highlands, British Columbia (with interval of sedimentation estimated to range from 52 to 44 Ma) (Selden and Penney 2009, Greenwood et al. 2016); and the Republic, Washington flora of the Klondike Mountain Formation (49.42 ± 0.54) (DeVore and Pigg 2010, Pigg et al. 2011). Relevant younger floras include the late Eocene Florissant flora in Colorado (ca. 34 Ma, Allen et al. 2020, MacGinitie 1953, Meyer 2003) and Oligocene Ruby and Beaverhead floras from western Montana (Becker 1961, 1969).

Similarities between the Kishenehn and earlier floras to the west, northwest and southeast of Kishenehn suggest that elements may have dispersed through the area and that the mountains at the time were not a fully effective dispersal barrier. Similarities between Kishenehn and coeval floras suggest that either there was still movement between floral elements or that climate conditions did not change enough to differentiate them. The presence of *Picea*, *Alnus*, *Thlaspi* and *Boniodendron* is evidence that these genera were already in Montana prior to the deposition of the Ruby flora.

With at least 107 entities, this is among the most diverse Eocene lacustrine megafossil plant assemblages known from North America and the most diverse Lutetian lacustrine deposit in the western US. The early Eocene Falkland flora of BC contains about 130 entities (Smith et al. 2009, 2012). In museum collections, up to 53 fruit and seed types have been recognized from the Parachute Creek member of the Green River Formation at Bonanza, Utah. Over 150 entities have been identified from the Republic flora (at the Stonerose Interpretive Center in Republic, WA and Burke Museum of

Natural History and Culture in Seattle, WA). The Kishenehn may be the most diverse assemblage, by proportion, of aquatic (13.7 %, 7 species) and herbaceous plants (11.8 %, 6 species). Two-thirds of the diversity (34 species) is made up of trees and 7.8 % is unknown.

Biogeographically, the Kishenehn flora includes many taxa that are Asian in their current distribution: *Ailanthus*, *Koeleruteria*, *Boniodendron*, *Dipteronia*, *Engelhardia* [*Palaeocarya*] and *Cercidiphyllaceae*. The biogeographic disjunct between paleofloras of western North America and modern floras of eastern Asia has long been acknowledged (MacGinitie 1933, Chaney 1940, Li 1952) and more recently reviewed (e.g., Manchester et al. 2009). What remains to be explored more is the spatial-temporal extirpation relationship of these taxa.

Conclusions

The Kishenehn flora is important for filling in the missing mid-Eocene floral record for the northern US Rocky Mountain region, helping to tell the story of Montana and Glacier National Park with an unusually high diversity of conifers, aquatic plants and herbaceous plants and complementing the record known from insects. We present our best estimate and the first quantitative estimates for the climate, which are consistent with floras “close” in space and time and with animals from the Kishenehn. Despite the 107 entities described here, including the oldest *Thlaspi*, many disseminules with uncertain affinities and leaves remain to be described. Many of the leaves have insect damage which needs to be analyzed. We are only beginning to scratch the surface of Kishenehn plants.

Acknowledgements

We thank Kurt Constenius for guidance in the field and sharing his knowledge of the regional geology and stratigraphy, Bill Rember for discussions on conifer identification, Dave Greenwood for suggestions on floristic comparisons and Nicole Neu-Yagle at the Denver Museum of Nature and Science for her guidance in the collections. We also thank Indah Huegele, Julian Correa-Narvaez and Ashley Hamersma for help in the field and Norm and Leona Constenius for their years of collecting. Special thanks to Kathleen Pigg and Christopher West for their time reviewing this very long manuscript and to Zuzana Heřmanová and Jan Sklenář for their hours of editing. All Specimens described in this study were collected in accordance with United States Forest Service Authorization HUN281.

References

Acosta, K., Appenroth, K. J., Borisjuk, L., Edelman, M., Heinig, U., Jansen, M. A., Oyama, T., Pasaribu, B., Schubert, I., Sorrels, S., Sree, K. S. (2021): Return of the Lemnaceae: Duckweed as a model plant system in the genomics and postgenomics era. – *The Plant Cell*, 33(10): 3207–3234.
<https://doi.org/10.1093/plcell/koab189>

Agricultura Romaneasca (2023): *Chemopodium polyspermum* L., spanac sălbatic [*Chemopodium polyspermum* L., wild spinach]. <http://www.agriculturaromaneasca.ro/produse/chemopodium-polyspermum-l-spanac-slbatic-3175-t10.html> [accessed 25 June 2023] (in Romanian)

Allen, S. E., Lowe, A. J., Peppe, D. J., Meyer, H. W. (2020): Paleoclimate and paleoecology of the latest Eocene Florissant flora of central Colorado, USA. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 551: 1–14.
<https://doi.org/10.1016/j.palaeo.2020.109678>

Areces-Berazain, F. (2022): *Chenopodiastrum murale* (nettle-leaf goosefoot).
<https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.12652> [accessed 25 June 2023].
<https://doi.org/10.1079/cabicompendium.12652>

Armstrong, W. P. (2021): Palomar College Wayne Armstrong’s treatment of the Lemnaceae.
<https://www2.palomar.edu/users/warmstrong/1wayindx.htm> [accessed 1 June 2022].

Axelrod, D. I. (1998): The Eocene thunder mountain flora of Central Idaho. – University of California Publications Geological Sciences, 142: 1–193.

Becker, H. F. (1959): A new species of *Mahonia* from the Ruby flora of southwestern Montana. – *Contributions from the Museum of Paleontology, University of Michigan*, 15(3): 33–38.

Becker, H. F. (1961): Oligocene plants from the upper Ruby River Basin, southwestern Montana. – *Geological Society of America Memoir*, 82: 1–127.
<https://doi.org/10.1130/mem82-p1>

Becker, H. F. (1969): Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. – *Palaeontographica*, 127B: 1–142.

Beilstein, M. A., Nagalingum, N. S., Clements, M. D., Mathews, S. (2010): Dated molecular phylogenies indicate a Miocene origin for *Arabidopsis thaliana*. – *Proceedings of the National Academy of Science*, 107(43): 18724–18728.
<https://doi.org/10.1073/pnas.0909766107>

Benet-Pierce, N., Simpson, M. G. (2014): The taxonomy of *Chenopodium desiccatum* and *C. nitens*, sp. nov. – *Journal of the Torrey Botanical Society*, 141(2): 161–172.
<https://doi.org/10.3159/torrey-d-13-00046.1>

Benkman, C. W. (1995): Wind dispersal capacity of pine seeds and the evolution of different seed dispersal modes in pines. – *Oikos*, 73: 221–224.
<https://doi.org/10.2307/3545911>

Berry, E. W. (1935): A preliminary contribution to the floras of the Whitemud and Ravenscrag Formations. – Canada Department of Mines, Bureau of Economic Geology, Geologic Survey, Memoir, 182: 1–109.
<https://doi.org/10.4095/100814>

Bhandari, S., Momohara, A., Paudyal, K. N. (2009): Late Pleistocene plant macro-fossils from the Gokarna formation of the Kathmandu Valley, Central Nepal. – *Bulletin of the Department of Geology*, 12: 75–88.
<https://doi.org/10.3126/bdg.v12i0.2252>

Bhandari, S., Paudyal, K. N., Momohara, A. (2010): Late Pleistocene plant macrofossils from the Thimi Formation

- (Madhyapur Thimi section) of the Kathmandu Valley, central Nepal. – *Journal of Nepal Geological Society*, 40: 31–48.
<https://doi.org/10.3126/jngs.v40i0.23594>
- Bhandari, S., Paudyal, K. N., Momohara, A. (2011): Climate change on the basis of plant macrofossil assemblages from the Late Quaternary sediments from the Mulpani section of the Gokarna Formation, Kathmandu Valley, Nepal. – *Journal of Stratigraphic Association of Nepal*, 7:47–58.
<https://doi.org/10.3126/jngs.v42i0.31440>
- Blackburn, D. T. (1982): Palaeobotany of coal-bearing strata from the Cretaceous and Tertiary of western Canada and Ellesmere Island. – Unpublished report to the Geological Survey of Canada, Institute of Sedimentary and Petroleum Geology, 128 pp.
- 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(9): 1389–1399.
<https://doi.org/10.3732/ajb.90.9.1389>
- Breedlovestrout, R. L. (2011): Paleofloristic studies in the Paleogene Chuckanut basin, western Washington, USA; Ph.D. Thesis. – MS, University of Idaho, Moscow, Idaho, 954 pp.
- Brown, R. W. (1929): Additions to the flora of the Green River Formation. – United States Geological Service Professional Paper, 154-J: 279–292.
<https://doi.org/10.3133/pp154j>
- Brown, R. W. (1939): Fossil fruits, leaves, and seeds of *Cercidiphyllum*. – *Journal of Paleontology*, 13(5): 485–499.
- Call, V. B., Dilcher, D. L. (1997): The fossil record of *Eucommia* (Eucommiaceae) in North America. – *American Journal of Botany*, 84(6): 798–814.
<https://doi.org/10.2307/2445816>
- Canadian Food Inspection Agency, (2017): Weed Seed: *Plantago lanceolata* (Ribgrass).
<https://inspection.canada.ca/plant-health/seeds/seed-testing-and-grading/seeds-identification/plantago-lanceolata/eng/1477312968602/1477312969103> [accessed 1 June 2022].
- Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., Ram, K. (2023): rgbi: Interface to the Global Biodiversity Information Facility API. R package version 3.7.7.
<https://CRAN.R-project.org/package=rgbi>.
- Chaney, R. W. (1940): Tertiary forests and continental history. – *Bulletin of the Geological Society of America*, 51(3): 469–488.
<https://doi.org/10.1130/gsab-51-469>
- Chen, Y., Manchester, S. R. (2015): Winged fruits of *Deviacer* in the Oligocene from the Ningming Basin in Guangxi, South China. – *PLoS ONE*, 10(12): 1–11.
<https://doi.org/10.1371/journal.pone.0144009>
- Spicer, R. A. (2011–2023): CLAMP on-line: <http://clamp.ibcas.ac.cn/Clampset2.html>. (accessed July 2021) [accessed 4 April 2023].
- Cleal, C. J., Thomas, B. A. (2010): Botanical nomenclature and plant fossils. – *Taxon*, 59(1): 261–268.
<https://doi.org/10.1002/tax.591024>
- Constenius, K. N. (1996): Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. – *Geological Society of America Bulletin*, 108: 20–39.
[https://doi.org/10.1130/0016-7606\(1996\)108<0020:lpecot>2.3.co;2](https://doi.org/10.1130/0016-7606(1996)108<0020:lpecot>2.3.co;2)
- Constenius, K. N., Dawson, M. R., Pierce, H. G., Walter, R. C. Wilson, M. V. H. (1989): Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia. – In: French, D. E., Grabb, R. F. (eds), *Field Conference Guidebook: Montana Centennial Edition*, Vol. 1. Geological Resources of Montana, pp. 189–203.
<https://doi.org/10.5962/p.215142>
- Corbett, S. L., Manchester, S. R. (2004): Phytogeography and history of *Ailanthus* (Simaroubaceae). – *International Journal of Plant Sciences*, 165(4): 671–690.
<https://doi.org/10.1086/386378>
- Crane, P. R., Stockey, R. A. (1985): Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the late Paleocene of Alberta, Canada. – *Canadian Journal of Botany*, 36(2): 340–364.
<https://doi.org/10.1139/b85-041>
- Crane, P. R., Stockey, R. A. (1986): Morphology and development of pistillate inflorescence in extant and fossil Cercidiphyllaceae. – *Annals of the Missouri Botanical Garden*. 73(2): 382–393.
<https://doi.org/10.2307/2399118>
- Crane, P. R., Stockey, R. A. (1987): *Betula* leaves and reproductive structures from the middle Eocene of British Columbia, Canada. – *Canadian Journal of Botany*, 65(12): 2490–2500.
<https://doi.org/10.1139/b87-338>
- Critchfield, W. B. (1975): Interspecific hybridization in *Pinus*: a summary review. – In: Fowler, D. P., Yeatman, C. Y. (eds), *Symposium on Interspecific and Interprovenance Hybridization in Forest Trees*. Proceedings of the 14th Meeting, Canada Tree Improvement Association, Part II, pp. 99–105.
- Currano, E. D., Labandeira, C. C., Wilf, P. (2010): Fossil insect folivory tracks paleotemperature for six million years. – *Ecological Monographs*, 80(4): 547–567.
<https://doi.org/10.1890/09-2138.1>
- Dawson, G. M. (1875): Report on the geology and resources of the region in the vicinity of the Forty-Ninth Parallel, from the Lake of the Woods to the Rocky Mountains. – Dawson Brothers, Montreal, 379 pp. + plates, maps and cross-sections.
<https://doi.org/10.5962/bhl.title.62419>
- Dawson, M. R., Constenius, K. N. (2018): Mammalian fauna of the middle Eocene Kishenehn Formation, Middle Fork of the Flathead River, Montana. – *Annals of Carnegie Museum*, 85(1): 25–60.
<https://doi.org/10.2992/007.085.0103>
- Del Rio, C., Wang, T. X., Liu, J., Liang, S. Q., Spicer, R. A., Wu, F. X., Zhou, Z. K., Su, T., (2020): *Asclepiadospermum* gen. nov., the earliest fossil record of Asclepiadoideae (Apocynaceae) from the early Eocene of central Qinghai-Tibetan Plateau, and its biogeographic implications. – *American Journal of Botany*, 107(1): 126–138.
<https://doi.org/10.1002/ajb2.1418>

- Denk, T., Dillhoff, R. M. (2005): *Ulmus* leaves and fruits from the early–middle Eocene of northwestern North America: systematics and implications for character evolution within Ulmaceae. – *Canadian Journal of Botany*, 83: 1663–1681.
<https://doi.org/10.1139/b05-122>
- DeVore, M. L., Pigg, K. B. (2010): Floristic composition and comparison of middle Eocene to late Eocene and Oligocene floras in North America. – *Bulletin of Geosciences*, 85(1): 111–134.
<https://doi.org/10.3140/bull.geosci.1135>
- DeVore, M. L., Taylor, W., Pigg, K. B. (2015): *Nuphar carlquistii* sp. nov. (Nymphaeaceae): a water lily from the latest early Eocene, Republic, Washington. – *International Journal of Plant Sciences*, 176 (4): 365–377.
<https://doi.org/10.1086/680482>
- Dillhoff, R. M., Dillhoff, T. A., Greenwood, D. R., DeVore, M. L., Pigg, K. B. (2013): The Eocene Thomas Ranch flora, Allenby Formation, Princeton, British Columbia, Canada. – *Botany*, 91(8): 514–529.
<https://doi.org/10.1139/cjb-2012-0313>
- Dillhoff, R. M., Leopold, E. B., Manchester, S. R. (2005): The McAbee flora of British Columbia and its relation to the early–middle Eocene Okanagan Highlands flora of the Pacific Northwest. – *Canadian Journal of Earth Sciences*, 42: 151–166.
<https://doi.org/10.1139/e04-084>
- Ding, W. N., Huang, J., Su, T., Xing, Y. W., Zhou, Z. K. (2018): An early Oligocene occurrence of the palaeoendemic genus *Dipteronia* (Sapindaceae) from Southwest China. – *Review of Palaeobotany and Palynology*, 249: 16–23.
<https://doi.org/10.1016/j.revpalbo.2017.11.002>
- Dorofeev, P. I. (1963): Tretichnye flory Zapadnoi Sibiri [The Tertiary floras of western Siberia]. – *Izdatelstvo Akademii nauk SSSR, Moscow*, 344 pp. (in Russian)
- eFloras (2008–2022): <http://www.efloras.org> [accessed 1 June 2022].
- Erwin, D. M., Schorn, H. E. (2005): Revisions of the conifers from the Eocene Thunder Mountain flora, Idaho, U.S.A. – *Review of Palaeobotany and Palynology*, 137: 125–145.
<https://doi.org/10.1016/j.revpalbo.2005.09.002>
- Falder, A. B., Stockey, R. A., Rothwell, G. W. (1999): In situ fossil seedlings of a *Metasequoia* like taxodiaceous conifer from Paleocene river floodplain deposits of central Alberta, Canada. – *American Journal of Botany*, 86(6): 900–902.
<https://doi.org/10.2307/2656710>
- Ferrucci, M. S. (2006): A new species of *Urvillea* (Sapindaceae) from northwestern Venezuela. – *Brittonia*, 58(1): 83–87.
[https://doi.org/10.1663/0007-196x\(2006\)58\[83:ansous\]2.0.co;2](https://doi.org/10.1663/0007-196x(2006)58[83:ansous]2.0.co;2)
- Fick, S. E., Hijmans, R. J. (2017): WorldClim 2: new 1 km spatial resolution climate surfaces for global land areas. – *International Journal of Climatology*, 37(12): 4302–4315.
<https://doi.org/10.1002/joc.5086>
- Gabr, D. G. (2014): Seed morphology and seed coat anatomy of some species of Apocynaceae and Asclepiadaceae. – *Annals of Agricultural Science*, 59(2): 229–238.
<https://doi.org/10.1016/j.aos.2014.11.010>
- GBIF (2023): <https://www.gbif.org> [accessed 5 May 2023].
- Golovneva, L. B., Alkseev, P. (2017): Taxonomy and morphological diversity of infructescences *Jenkinsella* co-occurred with *Trochodendroides* leaves in the Cretaceous and Paleogene. – *Palaeobotany*, 8: 92–121.
<https://doi.org/10.31111/palaeobotany/2017.8.92>
- Golovneva, L. B., Zolina, A. A. (2018): Fossil evidence of initial radiation of Cercidiphyllaceae. – *Paleobotanika*, 9: 54–75.
- Grande, L. (1984): Paleontology of the Green River Formation, with a review of the fish fauna. – *The Geological Survey of Wyoming, Bulletin no. 63, 2nd ed.*: 1–333.
- Greenwalt, D., Labandeira, C. (2013): The amazing fossil insects of the Eocene Kishenehn Formation in northwestern Montana. – *Rocks and Minerals*, 88(5): 434–441.
<https://doi.org/10.1080/00357529.2013.809972>
- Greenwalt, D., Goreva, Y., Siljeström, S., Rose, T., Harbach, R. E. (2013): Hemoglobin-derived porphyrins preserved in a middle Eocene blood-engorged mosquito. – *Proceedings of the National Academy of Sciences*, 110(46):18496–18500.
<https://doi.org/10.1073/pnas.1310885110>
- Greenwalt, D. E., Rose, T. R., Siljeström, S. M., Goreva, Y. S., Constenius, K. N., Wingerath, J. G. (2014): Taphonomy of the fossil insects of the middle Eocene Kishenehn Formation. – *Acta Palaeontologica Polonica*, 60(4): 931–947.
<https://doi.org/10.1139/cjes-2015-0157>
- Greenwalt, D. E., Rose, T. R., Chatzimanolis, S. (2016): Preservation of mandibular zinc in a beetle from the Eocene Kishenehn Formation of Montana. – *Canadian Journal of Earth Science*, 53:614–621.
<https://doi.org/10.1139/cjes-2015-0157>
- Greenwalt, D. E., Wingerath, J. G., Evenhuis, N. L. (2015): Two new and disparate fossil bee flies (Bombyliidae: Anthracinae) from the Americas and reassessment of *Anthrax dentoni* LEWIS, 1969. – *Palaeontologia Electronica*, 18.3.51A: 1–10.
<https://doi.org/10.26879/582>
- Greenwalt, D. E., Bickel, D. J., Kerr, P. H., Curler, G. R., Brown, B., De Jong, H., Fitzgerald, S. J., Dikow, T., Tkoč, M., Kehlmaier, C., Amorim, D. S. (2019): Diptera of the middle Eocene Kishenehn Formation. I. Documentation of diversity at the family level. – *Palaeontologia Electronica*, 22: 1–56.
<https://doi.org/10.26879/891>
- Greenwood, D. R. (1992): Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and tertiary palaeoclimates. – *Review of Palaeobotany and Palynology*, 71(1-4): 149–190.
[https://doi.org/10.1016/0034-6667\(92\)90161-9](https://doi.org/10.1016/0034-6667(92)90161-9)
- Greenwood, D. R., Archibald, S. B., Mathewes, R. W., Moss, P. T. (2005): Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. – *Canadian Journal of Earth Sciences*, 42(2): 167–185.
<https://doi.org/10.1139/e04-100>

- Greenwood, D. R., Pigg, K. B., Basinger, J. F., DeVore, M. L. (2016): A review of paleobotanical studies of the Early Eocene Okanogan (Okanogan) Highlands floras of British Columbia, Canada, and Washington, USA. – *Canadian Journal of Earth Sciences*, 53(6): 548–564. <https://doi.org/10.1139/cjes-2015-0177>
- Gregor, H. J. (1989): Aspects of the fossil record and phylogeny of the family Rutaceae (Zanthoxyleae, Toddalioideae). – *Plant Systematics and Evolution*, 162: 251–265. https://doi.org/10.1007/978-3-7091-3972-1_13
- Gregory, K. M. (1994): Palaeoclimate and palaeoelevation of the 35 ma Florissant flora, Front Range, Colorado. – *Palaeoclimates*, 1: 23–57.
- Griggs, P. H. (1970): Palynological interpretation of the type section, Chuckanut formation, Northwestern Washington. – In: Kosanke, R. M., Cross, A. T. (eds), *GSA Special Papers 127: Symposium on palynology of the Late Cretaceous and Tertiary*, pp. 169–112. <https://doi.org/10.1130/spe127-p169>
- Grimm, G. W., Potts, A. J., (2016): Fallacies and fantasies: the theoretical underpinnings of the Coexistence Approach for palaeoclimate reconstruction. – *Climate of the Past*, 12(3): 611–622.
- Grimm, G. W., Bouchal, J. M., Denk, T., Potts, A. (2016): Fables and foibles: a critical analysis of the Palaeoflora database and the Coexistence Approach for palaeoclimate reconstruction. – *Review of Palaeobotany and Palynology*, 233: 216–235. <https://doi.org/10.1016/j.revpalbo.2016.07.001>
- Guo, Q. (1998): Identification of weed seeds with colored pictures. – Chinese Agriculture Publishing House, Beijing, 176 pp.
- Harbach, R. E., Greenwalt, D. (2012): Two Eocene species of *Culiseta* (Diptera: Culicidae) from the Kishenehn Formation in Montana. – *Zootaxa*, 3530(1): 25–34. <https://doi.org/10.11646/zootaxa.3530.1.2>
- Haynes, R. R. (2020): *Elodea*. – In: Flora of North America Editorial Committee (ed.), *Flora of North America*, vol. 22. <http://floranorthamerica.org/Elodea> [accessed 2 June 2022]. <https://doi.org/10.1079/cabicompendium.112112>
- Haynes, R. R., Hellquist, C. B. (2020): *Alisma lanceolatum*. – In: Flora of North America Editorial Committee (ed.), *Flora of North America*, vol. 22. http://floranorthamerica.org/Alisma_lanceolatum [accessed 2 June 2022]. <https://doi.org/10.1079/cabicompendium.112112>
- Herendeen, P. S., Les, D. H., Dilcher, D. L. (1990): Fossil *Ceratophyllum* (Ceratophyllaceae) from the Tertiary of North America. – *American Journal of Botany*, 77: 7–16. <https://doi.org/10.1002/j.1537-2197.1990.tb13522.x>
- Herman, A. B., Spicer, R. A. (1996): Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. – *Nature*, 380(6572): 330–333. <https://doi.org/10.1038/380330a0>
- Hernandez-Castillo, G. R., Cevallos-Ferriz, S. R. S. (1999): Reproductive and vegetative organs with affinities to Haloragaceae from the Upper Cretaceous Huepac Chert Locality of Sonora, Mexico. – *American Journal of Botany*, 86(12): 1717. <https://doi.org/10.2307/2656670>
- Hickey, L. J. (1977). Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. – *Memoirs of the Geological Society of America*, 150: 1–181.
- Hijmans, R. (2023): raster: Geographic Data Analysis and Modeling. R package version 3.6-20, <https://CRAN.R-project.org/package=raster>.
- Hijmans R. J., Barbosa M., Ghosh A., Mandel A. (2023): geodata: Download Geographic Data. R package version 0.5-8, <https://CRAN.R-project.org/package=geodata>.
- Hill, S. R. (2022): *Malva*. – In: Flora of North America Editorial Committee (ed.), *Flora of North America*, vol. 6. <http://floranorthamerica.org/Malva> [accessed 2 June 2022]. <https://doi.org/10.1639/079.031.0307>
- Hoffman, G. L. (1995): Paleobotany and paleoecology of the Joffre Bridge Roadcut locality (Paleocene), Red Deer, Alberta; Master's Thesis. – MS, University of Alberta, Edmonton. <https://doi.org/10.1139/e99-095>
- Hopkins, W. S., Jr., Sweet, A. R. (1976): A microflora from a short section of the Paleogene Kishenehn Formation, southeastern British Columbia. – *Geological Survey of Canada, Paper 76-1 B*: 307–309. <https://doi.org/10.4095/104117>
- Huang, Y., Zhu, H., Su, T., Spicer, R. A., Hu, J., Jia, L., Zhou, Z. (2021): Rise of herbaceous diversity at the southeastern margin of the Tibetan Plateau: first insight from fossils. – *Journal of Systematics and Evolution*, 60(5): 1109–1123. <https://doi.org/10.1111/jse.12755>
- Huegele, I. B., Manchester, S. R. (2022): Newly recognized reproductive structures linked with *Langeria* from the Eocene of Washington, USA, and their affinities with Platanaceae. – *International Journal of Plant Sciences*, 183(5): 367–379. <https://doi.org/10.1086/720138>
- Iowa Plants (2012): *Typha angustifolia*. http://www.iowaplants.com/flora/family/Typhaceae/typha/t_angustifolia/Typha_angustifolia.html [accessed 1 June 2022]. https://doi.org/10.1007/978-3-319-26065-5_4
- Jepson, J. E., Makarkin, V. N. (2023): Fossil Neuropterida (Insecta: Neuroptera and Raphidioptera) from the middle Eocene Kishenehn Formation, Montana, USA. – *Zootaxa*, 5306(4): 427–444. <https://doi.org/10.11646/zootaxa.5306.4.2>
- Jijina, A. P., Currano, E. D., Constenius, K. (2019): The paleobotany and paleoecology of the Eocene Herren Beds of north-central Oregon, USA. – *Palaios*, 34(9): 424–436. <https://doi.org/10.2110/palo.2019.014>
- Kajita, Y., Suzuki, M. H., Nishida, H. (2021): A multicarpellary apocarpous gynoecium from the Late Cretaceous (Coniacian–Santonian) of the Upper Yezo Group of Obira, Hokkaido, Japan: *Obirafructus kokubunii* gen. et sp. nov. – *Acta Phytotaxonomica et Geobotanica*, 72(1): 1–21. <https://doi.org/10.18942/apg.202009>

- Kania-Kłosok, I., Krzemiński, W., Arillo, A. (2021): Two new long-rostrum crane fly species from the Cretaceous Iberian amber (Diptera, Limoniidae, Helius). – *Scientific Reports*, 11(1): 1–10.
<https://doi.org/10.1038/s41598-021-91803-1>
- Kirkbride, J. H., Jr., Gunn, C. R., Dallwitz, M. J. (2000 onwards): Family guide for fruits and seeds: descriptions, illustrations, identification, and information retrieval, 12th version.
<https://www.delta-intkey.com/famfs/index.htm> [accessed 1 June 2022].
- Kline, G. J., Sørensen, P. D. (2020): *Agrimonia*. – In: Flora of North America Editorial Committee (ed.), Flora of North America, vol. 9. <http://beta.floranorthamerica.org/Agrimonia> [accessed 25 June 2023].
<https://doi.org/10.1639/079.031.0307>
- Kodrul, T. M., Tekleva, M. V., Krassilov, V. A. (2006): A new conifer species, *Mesocyparis rosanovii* sp. nov. (Cupressaceae, Coniferales), and Transberingian floristic connections. – *Paleontological Journal*, 40(3): 93–102.
<https://doi.org/10.1134/s0031030106030142>
- Kong, M., Hong, S. (2016): A comparative study of fruit morphology of Boraginaceae in Korea. – *Symbolae Botanicae Upsalienses*, 38: 153–165.
- Koschnitzke, C. (2018): *Bradysia* sp. (Diptera: Sciaridae), a pollinator that can die in flowers of *Ditassa banksii* SCHULT. (Apocynaceae, Asclepiadoideae). – *Hoehnea*, 45: 126–128.
<https://doi.org/10.1590/2236-8906-61/2017>
- Kotthoff, U., Greenwood, D. R., McCarthy, F. M. G., Müller-Navarra, K., Prader, S., Hesselbo, S. P. (2014): Late Eocene to middle Miocene (33 to 13 million years ago) vegetation and climate development on the North American Atlantic coastal Plain (IODP Expedition 313, Site M0027). – *Climate of the Past*, 10: 1523–1539.
<https://doi.org/10.5194/cp-10-1523-2014>
- Kotyk, M. E. A., Basinger, J. F., McIver, E. E. (2003): Early Tertiary *Chamaecyparis* SPACH from Axel Heiberg Island, Canadian High Arctic. – *Canadian Journal of Botany*, 81: 113–130.
<https://doi.org/10.1139/b03-007>
- Kvaček, Z. (1995): *Limnobiophyllum* KRASSILOV – a fossil link between the Araceae and the Lemnaceae. – *Aquatic Botany*, 50(1): 49–61.
[https://doi.org/10.1016/0304-3770\(94\)00442-0](https://doi.org/10.1016/0304-3770(94)00442-0)
- Kvaček, Z., Wilde, V. (2010): Foliage and seeds of malvacean plants from the Eocene of Europe. – *Bulletin of Geosciences*, 85(1): 63–182.
- Kvaček, Z., Manchester, S. R., Schorn, H. E. (2000): Cones seeds and foliage from *Tetraclinis salicornioides* (Cupressaceae) from the Oligocene and Miocene of western North America: a geographic extension of the European Tertiary species. – *International Journal of Plant Sciences*, 161(2): 331–344.
- Kvaček, Z., Manchester, S. R., Akhmetiev, M. A. (2005): Review of the fossil history of *Craigia* (Malvaceae s.l.) in the Northern Hemisphere based on fruits and co-occurring foliage. *Modern Problems of Palaeofloristics, Palaeophytogeography, and Phytostratigraphy*. – *Transaction of the International Palaeobotanical Conference*, 1: 114–143.
<https://doi.org/10.1086/314245>
- Landolt, E. (2020): *Wolffiella*. – In: Flora of North America Editorial Committee (ed.), Flora of North America, vol. 22. <http://beta.floranorthamerica.org/Wolffiella> [accessed 2 June 2022].
<https://doi.org/10.1639/079.031.0307>
- LePage, B. A., Basinger, J. F. (1991): A new species of *Larix* (Pinaceae) from the early Tertiary of Axel Heiberg Island, Arctic Canada. – *Review of Palaeobotany and Palynology*, 70: 89–111.
[https://doi.org/10.1016/0034-6667\(91\)90080-m](https://doi.org/10.1016/0034-6667(91)90080-m)
- Lersten, N. R., Krueger, L., Curtis, J. D. (2002): Tracheoid variation among Bignoniaceae seed wings, with emphasis on *Campsis radicans*. – *International Journal of Plant Sciences*, 163(3): 369–378.
<https://doi.org/10.1086/339238>
- Lesquereux, L. (1878): Contributions to the fossil flora of the Western Territories. Part II. The Tertiary Flora. – *Report of the United States Geological Survey of the Territories*, 7: 1–366.
<https://doi.org/10.3133/70038957>
- Li, H. L. (1952): Floristic relationships between eastern Asia and eastern North America. – *Transactions of the American Philosophical Society*, 42(2): 371–429.
<https://doi.org/10.2307/1005654>
- Liang, M.-M., Bruch, A., Collinson, M., Mosbrugger, V., Li, C. S., Sun, Q. G., Hilton, J. (2003): Testing the climatic estimates from different palaeobotanical methods: an example from the Middle Miocene Shanwang flora of China. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 198: 279–301.
[https://doi.org/10.1016/s0031-0182\(03\)00471-1](https://doi.org/10.1016/s0031-0182(03)00471-1)
- Liu, X., Manchester, S. R., Jin, J. (2014): *Alnus* subgenus *Alnus* in the Eocene of western North America based on leaves, associated catkins, pollen, and fruit. – *American Journal of Botany*, 101(11): 1925–1943.
<https://doi.org/10.3732/ajb.1400228>
- Liu, Y., Basinger, J. F. (2009): *Metasequoia* HU et CHENG (Cupressaceae) from the Eocene of Axel Heiberg Island, Canadian High Arctic. – *Palaeontographica, Abteilung B*, 282(1-3): 69–97.
<https://doi.org/10.1127/palb/282/2009/69>
- Lowe, A. J., Greenwood, D. R., West, C. K., Galloway, J. M., Sudermann, M., Reichgelt, T. (2018): Plant community ecology and climate on an upland volcanic landscape during the early Eocene Climatic Optimum: McAbee Fossil Beds, British Columbia, Canada. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 511: 443–338.
<https://doi.org/10.1016/j.palaeo.2018.09.010>
- Ludvigsen, R. (2001): The fossils at Driftwood Canyon Provincial Park: a management plan for BC Parks.
<https://bvcentre.ca/files/External/FossilMgmtPlan-Ludvigsen2001.pdf> [accessed 2 June 2022].
- MacGinitie, H. D. (1933): The Trout Creek flora of southeastern Oregon. – *Carnegie Institution of Washington Publication*, 416, 68 pp.
- MacGinitie, H. D. (1953): Fossil plants of the Florissant Beds, Colorado. – *Carnegie Institution of Washington Publication*, 599, 198 pp.
- MacGinitie, H. D. (1969): The Eocene Green River flora of northwestern Colorado and northeastern Utah. –

- University of California Publications in Geological Science, 83: 1–202.
- MacGinitie, H. D. (1974): 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.
[https://doi.org/10.1016/0012-8252\(75\)90124-5](https://doi.org/10.1016/0012-8252(75)90124-5)
- Magallón-Puebla, S., Cevallos-Ferriz, S. R. (1994): *Eucommia constans* n. sp. fruits from upper Cenozoic strata of Puebla, Mexico: morphological and anatomical comparison with *Eucommia ulmoides* Oliver. – International Journal of Plant Sciences, 155(1): 80–95.
<https://doi.org/10.1086/297150>
- Mai, D. (1995): Tertiäre vegetationsgeschichte Europas: methoden und ergebnisse. – Gustav Fischer Verlag, Jena, Stuttgart, New York, 691 pp.
<https://doi.org/10.1002/fedr.4921060333>
- Manchester, S. R. (1986): Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America. – Botanical Gazette, 147: 200–225.
<https://doi.org/10.1086/337587>
- Manchester, S. R. (1987): The fossil history of the Juglandaceae. – Annals of the Missouri Botanical Garden, 21: 1–137.
- 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, vol. 2. Clarendon Press, Oxford, pp. 221–252.
<https://doi.org/10.2307/2807225>
- Manchester, S. R. (1994): Fruits and seeds from the middle Eocene Nut Beds Flora, Clarno Formation, Oregon. – Palaeontographica Americana, 58: 1–205.
- Manchester, S. R. (2000): Late Eocene fossil plants of the John Day Formation, Wheeler County, Oregon. – Oregon Geology, 62: 51–63.
- Manchester, S. R. (2001): Update on the megafossil flora of Florissant, Colorado. – In: Evanoff, E., Gregory-Wodzicki, K. M., Johnson, K. R. (eds), Fossil Flora and Stratigraphy of the Florissant Formation, Colorado. Denver Museum of Nature and Science, Denver, pp. 137–161.
[https://doi.org/10.1130/2008.2435\(04\)](https://doi.org/10.1130/2008.2435(04))
- Manchester, S. R., Chen, Z.-D., Lu, A.-M., Uemura, K. (2009): Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. – Journal of Systematics and Evolution, 47(1): 1–42.
<https://doi.org/10.1111/j.1759-6831.2009.00001.x>
- Manchester, S. R., Dilcher, D. L., Tidwell, W. D. (1986): Interconnected reproductive and vegetative remains of *Populus* (Salicaceae) from the middle Eocene Green River Formation, northeastern Utah. – American Journal of Botany, 73(1): 156–160.
- Manchester, S. R., Judd, W. S., Handley, B. (2006): Fruits and foliage of early poplars (Salicaceae: *Populus*) from the Eocene of Utah, Colorado and Wyoming. – International Journal of Plant Sciences, 167(4): 897–908.
<https://doi.org/10.1086/503918>
- Manchester, S. R., Dilcher, D. L., Tidwell, W. D. (1986): Interconnected reproductive and vegetative remains of *Populus* (Salicaceae) from the Middle Eocene Green River Formation, northeastern Utah. – American Journal of Botany, 73: 156–160.
<https://doi.org/10.1002/j.1537-2197.1986.tb09691.x>
- Manchester, S. R., O’Leary, E. L. (2010): Phylogenetic distribution and identification of fin-winged fruits. – Botanical Review, 76: 1–82.
<https://doi.org/10.1007/s12229-010-9041-0>
- Martinez, C. (2017): Passifloraceae seeds from the late Eocene of Colombia. – American Journal of Botany, 104(12): 1857–1866.
<https://doi.org/10.3732/ajb.1700224>
- Mathewes, R. W., Archibald, S. B., Lundgren, A. (2021): Tips and identification of early Eocene *Fraxinus* L. samaras from the Quilchena locality, Okanagan Highlands, British Columbia, Canada. – Review of Palaeobotany and Palynology, 293(1):104480.
<https://doi.org/10.1016/j.revpalbo.2021.104480>
- Mathewes, R. W., Greenwood, D. R., Archibald, S. B. (2016): Paleoenvironment of the Quilchena flora, British Columbia, during the early Eocene Climatic Optimum. – Canadian Journal of Earth Sciences, 53: 1–17.
<https://doi.org/10.1139/cjes-2015-0163>
- McClain, A. M., Manchester, S. R. (2001): *Dipteronia* (Sapindaceae) from the Tertiary of North American and implications for the phytogeographic history of the Aceroidae. – American Journal of Botany, 88(7): 1316–1325.
<https://doi.org/10.2307/3558343>
- McIver, E. E. (1992): Fossil *Fokienia* (Cupressaceae) from the Paleocene of Alberta, Canada. – Canadian Journal of Botany, 70(4): 742–749.
<https://doi.org/10.1139/b92-095>
- McIver, E. E., Basinger, J. F. (1987): *Mesocyparis borealis* gen. et sp. nov.: fossil Cupressaceae from the early Tertiary of Saskatchewan, Canada. – Canadian Journal of Botany, 65: 2338–2351.
<https://doi.org/10.1139/b87-318>
- McIver, E. E., Basinger, J. F. (1993): Fossil flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. – Palaeontographica Canadiana, 10: 1–167.
<https://doi.org/10.1139/b90-207>
- McIver, E. E., Basinger, J. F. (1999): Early Tertiary floral evolution in the Canadian high Arctic. – Annals of the Missouri Botanical Garden, 86(2): 523–545.
<https://doi.org/10.2307/2666184>
- McNair, D. M., Stults, D. Z., Axsmith, B., Alford, M. H., Starnes, J. E. (2019): Preliminary investigation of a diverse megafossil floral assemblage from the middle Miocene of southern Mississippi, USA. – Palaeontologica Electronica, 22.2.40A: 1–30.
<https://doi.org/10.26879/906>
- Meyer, H. W. (2003): Fossils of Florissant. – Smithsonian Books, New York, 272 pp.
- Meyer, H. W., Manchester, S. R. (1997): The Oligocene Bridge Creek Flora of the John Day Formation, Oregon. – University of California Press, Berkeley, Los Angeles, London, 354 pp.

- Minnesota Wildflowers a. (2023): *Carex oligocarpa* (Few-fruited Sedge). <https://www.minnesotawildflowers.info/grass-sedge-rush/few-fruited-sedge> [accessed 6 February 2023].
- Minnesota Wildflowers b. (2023): *Chenopodium pratericola* (Desert Goosefoot). <https://www.minnesotawildflowers.info/flower/desert-goosefoot> [accessed 25 June 2023].
- Mustoe, G. E., Dillhoff, R. M., Dillhoff, T. A. (2007): Geology and paleontology of the early Tertiary Chuckanut Formation. – In: Stelling, P., Tucker D. S. (eds), Floods, faults and fire: geological field trips in Washington State and southwest British Columbia, pp. 121–135. [https://doi.org/10.1130/2007.fld009\(06\)](https://doi.org/10.1130/2007.fld009(06))
- Myers, J. A. 1998. Paleovegetational heterogeneity and the record of Eocene-Oligocene climate change in the interior Pacific Northwest; Ph.D. Dissertation – MS, University of California, Santa Barbara, 503 pp.
- Native Plant Trust. (2023): *Alisma subcordatum* – southern water-plantain. <https://gobotany.nativeplanttrust.org/species/alisma/subcordatum> [accessed 1 May 2023]. <https://doi.org/10.2305/iucn.uk.2016-1.rlts.t64263394a67728483.en>
- Nichols, D. J. (2010): Reevaluation of the holotypes of the Wodehouse pollen species from the Green River Formation (Eocene, Colorado and Utah). – American Association of Stratigraphic Palynologists Contribution Series, 44, 97 pp.
- Nixon, K. C., Poole, J. M. (2003): Revision of the Mexican and Guatemalan species of *Platanus* (Platanaceae). – *Lundellia*, 6: 103–137. <https://doi.org/10.25224/1097-993x-6.1.4>
- Ollerton, J., Masinde, S., Meve, U., Picker, M., Whittington, A. (2009): Fly pollination in *Ceropegia* (Apocynaceae: Asclepiadoideae): biogeographic and phylogenetic perspectives. – *Annals of Botany*, 103(9): 1501–1514. <https://doi.org/10.1093/aob/mcp072>
- Ollerton, J., Winfree, R., Tarrant, S. (2011): How many flowering plants are pollinated by animals? – *Oikos*, 120(3): 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Orford, K. A., Murray, P. J., Vaughan, I. P., Memmott, J. (2016): Modest enhancements to conventional grassland diversity improve the provision of pollination services. – *Journal of Applied Ecology*, 53(3): 906–915. <https://doi.org/10.1111/1365-2664.12608>
- Pagliuso, D., Grandis, A., Igarashi, E. S., Lam, E., Buckeridge, M. S. (2018): Correlation of apiose levels and growth rates in duckweeds. – *Frontiers in Chemistry*, 6(291): 1–10. <https://doi.org/10.3389/fchem.2018.00291>
- Parker, W. H. (2021): *Larix laricina*. – Flora of North America Editorial Committee (ed.), Flora of North America, vol. 2. http://floranorthamerica.org/Larix_laricina [accessed 2 June 2022]. <https://doi.org/10.1639/079.031.0307>
- Pebesma, E., Bivand, R. (2005): Classes and methods for spatial data in R. – *R News*, 5(2): 9–13. <https://CRAN.R-project.org/doc/Rnews>.
- Penhallow, D. P. (1908): Report on Tertiary plants of British Columbia collected by Lawrence M. Lambe in 1906 together with a Discussion on previously recorded Tertiary floras. – Canada Department of Mines Geological Survey Branch, 1013: 1–157. <https://doi.org/10.4095/106549>
- Peppe, D. J., Baumgartner, A., Flynn, A., Blonder, B. (2018): Reconstructing paleoclimate and paleoecology using fossil leaves. – In: Croft, D., Su, D., Simpson, S. (eds), *Methods in paleoecology*. Springer, Cham, pp. 289–317. https://doi.org/10.1007/978-3-319-94265-0_13
- Perkins, A. J. (2019): Nomenclatural updates and a new species of annual *Hydrocotyle* (Araliaceae) from Western Australia. – *Nuytsia*, 30: 253–277. <https://doi.org/10.58828/nuy00925>
- Pierce, H. G., Constenius, K. N. (2001): Late Eocene-Oligocene nonmarine mollusks of the northern Kishenehn Basin, Montana and British Columbia. – *Annals of Carnegie Museum Pittsburgh*, 70(1): 1–112. <https://doi.org/10.5962/p.215142>
- Pierce, H. G., Constenius, K. N. (2014): Terrestrial and aquatic mollusks of the Eocene Kishenehn Formation, Middle Fork Flathead River, Montana. – *Annals of Carnegie Museum*, 82(4): 305–329. <https://doi.org/10.2992/007.082.0401>
- Pigg, K. B., DeVore, M. L. (2016): A review of the plants of the Princeton chert (Eocene, British Columbia, Canada). – *Botany*, 94: 661–681. <https://doi.org/10.1139/cjb-2016-0079>
- Pigg, K. B., DeVore, M. L., Wojciechowski, M. F. (2008): *Paleosecuridaca curtisii* gen. et sp. nov., *Securidaca*-like samaras (Polygonaceae) from the late Paleocene of North Dakota and their significance to the divergence of families within the Fabales. – *International Journal of Plant Sciences*, 169(9): 1304–1313. <https://doi.org/10.1086/591981>
- Pigg, K. B., DeVore, M. L., Volkman, K. E. (2011): Fossil Plants from Republic: A Guidebook. – Stonerose Interpretive Center, Republic, Washington, 86 pp.
- Pigg, K. B., Wehr, W. C. (2002): Tertiary flowers, fruits and seeds of Washington and adjacent areas, part III. – *Washington Geology*, 30(3-4): 3–16.
- Povey, D. A. R., Spicer, R. A., England, P. C. (1994): Palaeobotanical investigations of early Tertiary palaeoelevations in northeastern Nevada: initial results. – *Review of Palaeobotany Palynology*, 81: 1–10. [https://doi.org/10.1016/0034-6667\(94\)90122-8](https://doi.org/10.1016/0034-6667(94)90122-8)
- Puri, G. S. (1951): Fossil fruits of *Trapa* and remains of other fresh-water plants from the Pleistocene of Kashmir. – *The Journal of the Indian Botanical Society*, 30(1-4): 113–121.
- R Core Team (2022): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reichgelt, T., West, C. K., Greenwood, D. R. (2018): The relation between global palm distribution and climate. – *Scientific Reports*, 8(4721): 1–11. <https://doi.org/10.1038/s41598-018-23147-2>
- Reid, E. M., Chandler, M. E. J. (1933): London clay flora. – British Museum of Natural History, London, 594 pp. <https://doi.org/10.5962/bhl.title.110147>

- Robil, J. M., Gao, K., Neighbors, C. M., Boeding, M., Carland, F. M., Bunyak, F., McSteen, P. (2021): GRASVIQ: an image analysis framework for automatically quantifying vein number and morphology in grass leaves. – *The Plant Journal*, 107(2): 1–20.
<https://doi.org/10.1111/tpj.15299>
- Royer, D. L., Sack, L., Wilf, P., Cariglino, B., Lusk, C. H., Wright, I. J., Westoby, M., Jordan, G. J., Niinemets, Ü., Coley, P. D., Cutter, A. D. (2007): Fossil leaf economics quantified: calibration, Eocene case study, and implications. – *Paleobiology*, 33(4): 574–589.
<https://doi.org/10.1666/07001.1>
- Scudder, G. G. E., Cannings, R. A. (2006): The diptera families of British Columbia. – *British Columbia Ministry of Forest*, 1(158): 1–163.
- Selden, P. A., Penney, D. (2009): A fossil spider (Araneae: Pisauridae) of Eocene age from Horsefly, British Columbia, Canada. – *Contributions to Natural History*, 12: 1269–1282.
- Sherman-Broyles, S. L. (2021): *Ulmus glabra*. – *Flora of North America Editorial Committee (ed.), Flora of North America*, vol. 3. http://floranorthamerica.org/Ulmus_glabra [accessed 2 June 2022].
<https://doi.org/10.1639/079.031.0307>
- Silba, J. (1986): An international census of the Coniferae. – *Phytologia memoir no. 8*, H. N. Moldenke and A. L. Moldenke, Corvallis, Oregon, 217 pp.
- Singh, S. P., Gumber, S., Singh, R. D., Pandey, R. (2021): Differentiation of diploxylon and haploxylon pines in spatial distribution, and adaptational traits. – *Acta Ecologica Sinica*, 43(1): 1–10.
<https://doi.org/10.1016/j.chnaes.2021.07.007>
- Smith, R. Y., Basinger, J. F., Greenwood, D. R. (2009): Depositional setting, fossil flora, and paleoenvironment of the Early Eocene Falkland site, Okanagan Highlands, British Columbia. – *Canadian Journal of Earth Sciences*, 46(11): 811–822.
<https://doi.org/10.1139/e09-053>
- Smith, R. Y., Basinger, J. F., Greenwood, D. R. (2012): Early Eocene plant diversity and dynamics in the Falkland flora, British Columbia, Canada. – *Palaeobiodiversity and Palaeoenvironments*, 92: 309–328.
<https://doi.org/10.1007/s12549-011-0061-5>
- Soza, V. L., Haworth, K. L., Di Stilio, V. S. (2013): Timing and consequences of recurrent polyploidy in meadow-rues (*Thalictrum*, Ranunculaceae). – *Molecular Biology and Evolution*, 30(8): 1940–1954.
<https://doi.org/10.1093/molbev/mst101>
- Spicer, R. A., Valdes, P. J., Spicer, T. E. V., Craggs, H. J., Srivastava, G., Mehrotra, R. C., Yang, J. (2009): New developments in CLAMP: calibration using global gridded meteorological data. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 283(1–2): 91–98.
<https://doi.org/10.1016/j.palaeo.2009.09.009>
- Stockey, R. A., Hoffman, G. L., Rothwell, G. W. (1997) The fossil monocot *Limnobiophyllum scutatum*: resolving the phylogeny of Lemnaceae. – *American Journal of Botany*, 84(3): 355–368.
<https://doi.org/10.2307/2446009>
- Szafer, W. (1961): Miocenska flora ze Starych Gliwic na Śląsku [Miocene flora from Old Gliwice in Silesia]. – *Wydawnictwa Geologiczne, Warszawa*, 251 pp. (in Polish)
<https://doi.org/10.5586/mb.1958.006>
- Takhtajan, A. (1982): *Ulmaceae-Betulaceae*. – *Iskopaemye cbetkovye rasteniya SSSR [Fossil flowering plants of the USSR]*, vol. 2. – Nauka, Leningrad, p. 216.
<https://doi.org/10.1002/fedr.4910960520> (in Russian)
- Taylor, R. J. (2021): *Picea mariana*. – *Flora of North America Editorial Committee (ed.), Flora of North America*, vol. 2. http://floranorthamerica.org/Picea_mariana [accessed 2 June 2022].
<https://doi.org/10.1639/079.031.0307>
- Thomas, P. A., Stone, D., La Porta, N. (2018): Biological flora of the British Isles: *Ulmus glabra*. – *Journal of Ecology*, 106(4): 1724–1766.
<https://doi.org/10.1111/1365-2745.12994>
- TMI (2022): Plant macrofossils: show unique identification. <https://tmi.laccore.umn.edu/uniqueIdentification/show/136#1057> [accessed 2 June 2022].
- Traiser, C., Dalitz, H., Krause, M., Lange, J., Roth-Nebelsick, A., Kovar-Eder, J. (2019): Digiphyll – a digital tool for competence building in palaeobotany for teaching and research, version 1.0. <http://digiphyll.smns-bw.org> [accessed 2 February 2023].
- Van der Wall, S. B. (1992): The role of animals in dispersing a “wind-dispersed” pine. – *Ecology*, 73(2): 614–621.
<https://doi.org/10.2307/1940767>
- Vescovo, S. V. (2023): *Cycloloma atriplicifolium* (SPRENG.) J.M.COULT.
<https://luirig.altervista.org/schedenam/fnam.php?taxon=Cycloloma+atriplicifolium> [accessed 25 June 2023].
<https://doi.org/10.1079/cabicompendium.116865>
- Wang, B., Zhang, S., Zhang, P., Yang, Y., Chen, J., Zhang, Y., Xie, S. (2021). A new occurrence of *Craigia* (Malvaceae) from the Miocene of Yunnan and its biogeographic significance. – *Historical Biology*, 33(12): 3402–3412.
<https://doi.org/10.1080/08912963.2020.1867980>
- Wang, Q., Manchester, S. R., Gregor, H., Shen, S., Li, Z. (2013): Fruits of *Koelreuteria* (Sapindaceae) from the Cenozoic throughout the Northern Hemisphere: their ecological, evolutionary, and biogeographic implications. – *American Journal of Botany*, 100(2): 422–449.
<https://doi.org/10.3732/ajb.1200415>
- Wheeler, E. A., Manchester, S. R. (2002): Woods of the middle Eocene nut beds flora, Clarno Formation, Oregon, USA. – *IAWA Journal, Supplement 3*: 1–188.
<https://doi.org/10.1017/s0022336000044619>
- Wickham, H. (2016): *ggplot2: Elegant Graphics for Data Analysis*. – Springer-Verlag, New York, 213 pp.
- Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D. (2023): *dplyr: A Grammar of Data Manipulation*. R package version 1.1.2.
<https://CRAN.R-project.org/package=dplyr>
- Wiemann, M. C., Manchester, S. R., Dilcher, D. L., Hinojosa, L. F., Wheeler, E. A. (1998): Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. – *American Journal of Botany*, 85(12): 1796–1802.
<https://doi.org/10.2307/2446514>
- Wilde, V., Frankenhäuser, H. (1998): The middle eocene plant taphocoenosis from Eckfeld (Eifel, Germany). –

- Review of Palaeobotany and Palynology, 101(1-4): 7–28.
[https://doi.org/10.1016/s0034-6667\(97\)00067-5](https://doi.org/10.1016/s0034-6667(97)00067-5)
- Wilson, L. R., Webster, R. M. (1946): Plant microfossils from a Fort Union coal of Montana. – *American Journal of Botany*, 33: 271–278.
<https://doi.org/10.1002/j.1537-2197.1946.tb10375.x>
- Wing, S. L. (1987): Eocene and Oligocene floras of the Rocky Mountains. – *Annals of the Missouri Botanical Garden*, 74(4): 748–784.
<https://doi.org/10.2307/2399449>
- Wing, S. L., Greenwood, D. R. (1993): Fossils and fossil climate: the case for equable continental interiors in the Eocene. – *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 341(1297): 243–252.
<https://doi.org/10.1098/rstb.1993.0109>
- Wodehouse, R. P. (1933): The oil shales of the Eocene Green River formation. – *Bulletin of the Torrey Botanical Club*, 60(7): 479–524.
<https://doi.org/10.2307/2480586>
- Wolfe, J. A. (1971): Tertiary climatic fluctuations and methods of analysis of Tertiary floras. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 9(1): 27–57.
[https://doi.org/10.1016/0031-0182\(71\)90016-2](https://doi.org/10.1016/0031-0182(71)90016-2)
- Wolfe, J. A. (1997): Relations of environmental change to angiosperm evolution during the late Cretaceous and Tertiary. – In: Iwatsuki, K., Raven, P. H. (eds), *Evolution and diversification of land plants*, Tokyo: Springer Japan, pp. 269–290.
- Wolfe, J. A., Schorn, H. E. (1990): Taxonomic revision of the Spermatopsida of the Oligocene Creede flora, Southern Colorado. – *U.S. Geological Survey Bulletin*, 1923: 1–69.
<https://doi.org/10.3133/b1923>
- Wolfe, J. A., Wehr, W. (1987): Middle Eocene dicotyledonous plants from Republic, northeastern Washington. – *U.S. Geological Survey Bulletin*, 1597: 1–58.
<https://doi.org/10.3133/b1597>
- Wu, J., Ding, S., Li, Q., Zhao, Z., Sun, B. (2014): First occurrence of *Platykladus* from the Upper Miocene of southwest China and its phytogeographic implications. – *PLOS ONE*, 9(12): e115141.
<https://doi.org/10.1371/journal.pone.0115141>
- Wu, M., Huang, J., Su, T., Zhou, Z., Xing, Y. (2021): *Fraxinus* L. (Oleaceae) fruits from the early Oligocene of southwest China and their biogeographic implications. – *Fossil Imprints*, 77(2): 287–298.
<https://doi.org/10.37520/fi.2021.021>
- Zacharias, E. H. (2012): *Atriplex Stutzia covillei*. – In: *Jepson Flora Project* (eds), *Jepson eFlora*.
https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=95111 [accessed June 25 2023].
- Zhang, J., Li, X., Xu, X., Chen, H., Li, Y., Guy, R. D. (2021): Leaf morphology, photosynthesis and pigments change with age and light regime in savin juniper. – *Plant Biology*, 23(6): 1097–1108.
<https://doi.org/10.1111/plb.13256>
- Zhu, H., Huang, Y., Su, T., Zhou, Z. (2016): New fossil seeds of *Eurya* (Theaceae) from East Asia and their paleobiogeographic implications. – *Plant diversity*, 38(3): 125–132.
<https://doi.org/10.1016/j.pld.2016.05.001>

Appendix I

Sources of data and imagery consulted on extant genera.

- GBIF.org. 2023. GBIF Occurrence Download. *Dipteronia*. <https://doi.org/10.15468/dl.x8b5cm> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Metasequoia*. <https://doi.org/10.15468/dl.wcnqqu> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Spirodela*. <https://doi.org/10.15468/dl.z54fpa> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Equisetum*. <https://doi.org/10.15468/dl.j9kyd8> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Juniperus*. <https://doi.org/10.15468/dl.v33d2g> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Abies*. <https://doi.org/10.15468/dl.w9s6df> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Larix*. <https://doi.org/10.15468/dl.nj6t9k> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Pinus*. <https://doi.org/10.15468/dl.5aemj7> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Picea*. <https://doi.org/10.15468/dl.9eucnr> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Lemna*. <https://doi.org/10.15468/dl.zeydnx> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Wolffiella*. <https://doi.org/10.15468/dl.qugyqh> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Potamogeton*. <https://doi.org/10.15468/dl.td5pfp> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Typha*. <https://doi.org/10.15468/dl.gfpmyj> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Ceratophyllum*. <https://doi.org/10.15468/dl.vx8w7y> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Thalictrum*. <https://doi.org/10.15468/dl.5u9muk> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Platanus*. <https://doi.org/10.15468/dl.e9esf8> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Myriophyllum*. <https://doi.org/10.15468/dl.8wj7uk> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Cercidiphyllum*. <https://doi.org/10.15468/dl.3rbdag> [accessed 5 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Populus*. <https://doi.org/10.15468/dl.mfbzxs> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Agrimonia*. <https://doi.org/10.15468/dl.ghxw7> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Ulmus*. <https://doi.org/10.15468/dl.3c9e9z> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Celtis*. <https://doi.org/10.15468/dl.megh7w> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Alnus*. <https://doi.org/10.15468/dl.ddh8eq> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Betula*. <https://doi.org/10.15468/dl.gbz7q6> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Boniodendron*. <https://doi.org/10.15468/dl.4pjafc> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Ailanthus*. <https://doi.org/10.15468/dl.e3dct5> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Cedrela*. <https://doi.org/10.15468/dl.jyfgxq> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Thlaspi*. <https://doi.org/10.15468/dl.322wag> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Chenopodium*. <https://doi.org/10.15468/dl.27xf9j> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Eucommia*. <https://doi.org/10.15468/dl.4x46de> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Fraxinus*. <https://doi.org/10.15468/dl.kzdpmj> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Catalpa*. <https://doi.org/10.15468/dl.um86yk> [accessed 6 May 2023].
- GBIF.org. 2023. GBIF Occurrence Download. *Chilopsis*. <https://doi.org/10.15468/dl.ugwazw> [accessed 6 May 2023].