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THE EARLY EOCENE FLORA OF HORSEFLY, BRITISH COLUMBIA, CANADA AND ITS PHYTOGEOGRAPHIC SIGNIFICANCE

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Abstract: About forty species, including a bryophyte, ferns, conifers, *Ginkgo*, and over 35 angiosperms, are recognized based on compression-impression remains from the early Eocene of Horsefly, British Colombia, Canada. This flora is in the north central part of a chain of late early Eocene fossil assemblages known as floras of the "Okanagan Highlands" (= "Okanogan Highlands" in the US). These floras extend from north central British Columbia, Canada southeast to Republic, Washington, USA. The Horsefly flora shows similarities to other Eocene Okanagan Highlands floras, such as McAbee, Falkland, Thomas Ranch and Republic, but with some additional rare taxa. In the broader sense, the Horsefly flora can be compared with early and middle Eocene floras of eastern Asia and midcontinental North America, but shares fewer elements with Europe. *Ginkgo*, *Metasequoia*, *Pinus*, *Palaeocarpinus*, ulmaceous leaves and *Deviacer* are shared with northeastern China as well as western North American sites. *Fagopsis*, *Macginitiea*, *Dipteronia*, *Florissantia*, *Sassafras* and *Lagokarpos* also occur in other western North American Eocene floras and *Koelreuteria* and *Jenkinsella* with Eocene paleofloras of China. These comparisons demonstrate probable floristic exchange between northwestern North America and northeastern China via a Beringian route during the late early Eocene.

Key words: Okanagan (Okanogan) Highlands, early Eocene, high elevation fossil floras, biogeography

Introduction

The Horsefly fossil flora is one of many plant fossil assemblages of the Okanagan Highlands (US spelling "Okanogan Highlands"), a regional uplift ca. 1400 km long extending from central British Columbia, Canada into northeastern Washington, USA (Text-fig. 1). The Okanagan Highlands floras also include sites in British Columbia, Canada at Driftwood Canyon, Joseph Creek, Chu Chua (e.g., Wolfe and Tanai 1987), McAbee (Dillhoff et al. 2005); Falkland (Smith et al. 2012); Quilchena (Mathewes et al. 2016); the Allenby Formation in and around Princeton, [e.g., Thomas Ranch (Dillhoff et al. 2013), One Mile Creek (Crane and Stockey 1986) and the Princeton chert (Pigg and DeVore 2016)], and the Republic flora of northeastern Washington, USA (Wolfe and Wehr 1987, DeVore and Pigg 2010). Current and previously studied plant-bearing localities, their history of collecting, and floral composition were reviewed by Greenwood et al. (2016).

Exposures of shale near Horsefly are well known for beautifully preserved fish and insects (Wilson 1977a, b, c,

Text-fig. 1. Map of the early Eocene Okanagan Highlands British Columbia, Canada and Washington, United States of America. Modified from Archibald et al. 2014: fig. 2, courtesy of Bruce Archibald.

1993, Archibald et al. 2011, for summaries). Fossil plant remains were first noted from Horsefly by Penhallow (1902) who subsequently recognized more than 50 species (Penhallow 1908). Since then, with the collection of many additional specimens, and allowing for intraspecific variation, approximately 40 plant taxa are now recognized, including a bryophyte, several ferns, *Ginkgo* L., conifers (taxodioid Cupressaceae, Pinaceae and Taxaceae), and more than 15 angiosperm families. Both vegetative and reproductive remains are known for several families, including some well preserved flowers with *in situ* pollen. Preliminary lists of plant megafossils from Horsefly were summarized by Greenwood et al. (2005), and palynomorphs by Moss et al. (2005).

Taxa occurring at Horsefly that have been published or mentioned previously include the moss *Aulacomnium heterostichiodes* J.B.JANSSENS, D.G.HORTON et BASINGER (Janssens et al. 1979) and the angiosperms *Pistillipollianthus wilsonii* STOCKEY et MANCHESTER [a flower with in situ *Pistillipollenites macgregori* ROUSE pollen (Stockey and Manchester 1988)], fruits of *Ulmus* L. (Manchester 1989a), *Dipteronia* OLIV. (Manchester and McClain 2001) and *Lagokarpos lacustris* D.M.MCMURRAN et MANCHESTER (McMurran and Manchester 2010), pistillate and staminate reproductive structures of *Palaeocarpinus* P.R.CRANE (Douglas and Stockey 1996, Pigg et al. 2003, Correa-Narvaez and Manchester 2021) and tiny seeds now designated as *Pteroheterochrosperma horseflyensis* MACK.A.SM., GREENWALT et MANCHESTER (Smith et al. 2023). However, a comprehensive treatment of the Horsefly flora has been lacking. The purpose of this article is to provide an updated report on the floristic composition of the Horsefly plant fossil assemblage, based on an increased collection of megafossils, and to consider its phytogeographic implications. The flora shares many taxa with other Okanagan Highlands sites but also contains several rare forms of uncertain affinities, broadening our understanding of the diversity of the Okanagan Highlands biota.

Material and methods

The Horsefly flora is found in exposures along the Horsefly River approximately 8 km north and east of the town of Horsefly, in the Cariboo region of south central British Columbia, Canada (Text-fig. 1; Wilson 1977b, 1993, Greenwood et al. 2005, 2016). Plant fossils are found, along with fish and insects, in shales of an unnamed formation, for which no radiometric dates are available. Other Okanagan floras of similar composition that have been dated radiometrically are placed in the second half of the early Eocene, or middle to late Ypresian, mostly approximately 51 Ma (e.g., Rubino et al. 2021). Fossiliferous units in the Okanagan Highlands were deposited within en echelon grabens and half grabens formed as the result of four significant crustal processes: 1) regional extension, 2) metamorphic core complex emplacement, 3) plutonism, and 4) volcanism, in addition to lakes formed by damming of rivers by lava flows from volcanism associated with uplift (Morris and Hooper 1997, Ickert et al. 2009). Resulting from these dynamic forces was an Eocene topography of

Table 1. List of floral elements described from the Horsefly assemblage. * = reported from Horsefly previously.

Bryophytopsida
      Aulacomnium heterostichiodes J.B.JANSSENS, D.G.HORTON et BASINGER
Pteridopsida
    Filicalean Fern #1
    Filicalean Fern #2
    Salviniaceae
      Azolla primaeva (PENH.) C.A.ARNOLD
Coniferopsida
    Cupressaceae
      Metasequoia occidentalis (J.S.NEWBERRY) R.W.CHANEY
      Taxoidioid conifer foliage, seed and pollen cones
      Chamaecyparis SPACH
    Pinaceae
      Pinus L. 3- to 5-needle forms
      Pinus L. (section *Diploxylon*) disarticulated, winged seeds
      Coniferous winged seeds
    Taxaceae
      Amentotaxis PILG.
Ginkgopsida
    Ginkgoaceae
      Ginkgo biloba L.
Magnoliopsida
Monocotyledonae
      Monocot #1 –broad-leaved
      Monocot #2 – parallel veined
      Monocot #3 – parallel veined
"Dicots"
    Lauraceae
      Sassafras hesperia (E.W.BERRY) J.A.WOLFE et WEHR
      cf. *Lindera* THUMB.
    Platanaceae
      Macginitiea gracilis J.A.WOLFE et WEHR
      Macginicarpa J.A.WOLFE et WEHR
      Platanaceous fruits
    Cercidiphyllaceae
      Trochodendroides E. W. BERRY
      Jenkinsella E.REID et M.CHANDLER
    Betulaceae
      Corylites J.S.GARDNER
      Alnus parvifolia (E.W.BERRY) J.A.WOLFE et WEHR
      Palaeocarpinus barksdalae PIGG, MANCHESTER et WEHR
    Fagaceae
      Fagopsis undulata (KNOWLT.) J.A.WOLFE et WEHR
    Anacardiaceae
      Rhus L.
      cf. *Schinus* L.
    Sapindaceae
      Acer L.
      Dipteronia brownii MANCHESTER
      Koelreuteria dilcheri Q.WANG, MANCHESTER, H.-J.GREGOR, S.SHEN et Z.Y.LI
    Polygalaceae
      Deviacer wolfei MANCHESTER
    Malvaceae
      Florissantia quilchenensis (MATHEWES et R.C.BROOKE) MANCHESTER
    Ulmaceae
      Ulmus L.
      Cedrelospermum SAPORTA
    Rosaceae
      cf. *Rubus* L.
      Photinia pageae J.A.WOLFE et WEHR
      Prunus L.
      cf. *Hesperomeles* LINDL.
    Incertae sedis – leaves
      Averrhoites L.HICKEY
      Flowers, Fruits and Seeds
      Pistillipollianthus wilsonii STOCKEY et MANCHESTER
      Flowers with many stamens types 1 and 2
      Pteroheterochrosperma horseflyensis MACK.A.SM., GREENWALT et MANCHESTER
      Lagokarpos D.M.MCMURRAN et MANCHESTER
      cf. Apiaceae fruit

Text-fig. 2. Ferns, *Ginkgo*, and taxodioid conifers. a: Filicalean fern type 1. UAPC-ALTA S sn. b, c: Filicalean fern type 2. b: Overview of specimen, UAPC-ALTA S 59515. c: Detail of (b) to show pinnule shape. d: *Azoll*a *primaeva*, small plant fragments and rhizoids, BBM-PAL-P000002. e: *Metasequoia occidentalis* twig with leafy branchlets, BBM- PAL-P000003. f: *Ginkgo biloba* leaf showing dichotomous venation, GSC 7567. g: Taxodioid branches with flared shoot apices that may represent small cones, UAPC-ALTA S 25090. h: *Metasequoia occidentalis* branchlet showing opposite leaves, UAPC-ALTA S 59495. i: Taxodioid branchlet showing variation, BBM-PAL-P000004. j: Taxodioid pollen cone, BBM-PAL-P000045. k: *Metasequoia* seed cone, BBM-PAL-P000005 A. l: cf. *Chamaecyparis*, BBM-PAL-P000006. Scale bars: a–c, f–l = 1 cm, d = 0.5 cm, e = 2 cm.

mountains of high relief similar to those of the modern British Columbian Coast and Selkirk ranges. These ranges, and associated highland plateaus, were dissected by deeply cut waterways (Tribe 2005, Archibald et al. 2011).

Original specimens of Penhallow (1902, 1908) were examined and photographed at the Geological Survey of Canada, Ottawa (prefixed GSC). Specimens were studied from the Paleobotanical Collection of the University of

Alberta, Edmonton (prefixed UAPC-ALTA). Many of these specimens were collected and donated by Mark V. H. Wilson, with additional collections made by Ruth A. Stockey and colleagues in 1998. Other specimens, collected by Bruce Archibald, are deposited at the Beaty Biodiversity Museum, University of British Columbia, Vancouver, BC, Canada (prefixed BBM), and at the Royal British Columbia Museum, Victoria, BC, Canada (prefixed RBCM).

Results

The Horsefly flora contains a diverse assemblage of around 40 taxa including a bryophyte, ferns, conifers, *Ginkgo*, and angiosperms (Table 1).

Bryophytes

A bryophyte was described previously (Janssens et al. 1979). *Aulacomnium heterostichioides* was based on a single specimen and compared with extant moss, *Aulacomnium heterostichium* (Hedw.) Bruch et Schimp.

Pteridophytes

Ferns. Several specimens of fern foliage have been collected, representing at least two filicalean types, along with one heterosporous water fern (Text-fig. 2a–d). One of the filicalean ferns is represented by an incomplete specimen 8 cm long with a prominent rachis around 1 mm thick with widely separated pinnae up to around 2.7 cm apart. Pinnae have an equally thick rachis of 1 mm that bear up to five paired, terminal, slightly lobed pinnules around 1.5 cm long that terminate in pointed tips, and have strong dichotomous venation (Text-fig. 2a). The second filicalean foliage type is based on a specimen ca. 6 cm long having crowded, lobed pinnae that are oriented apically with dichotomous venation (Text-fig. 2b, c). No fertile specimens of these two fern types from Horsefly or other Okanagan Highlands sites are known to date. *Azolla primaeva* (Penh.) C.A.Arnold, the heterosporous water fern known from many of the other Okanagan Highlands sites (Arnold 1955), is found commonly in its characteristic mats at this locality (Text-fig. 2d).

Gymnosperms

Ginkgoaceae. *Ginkgo biloba* L. is represented by a few small undivided to slightly lobed leaves showing the typical fan-like outline and radiating dichotomous venation characteristic of the genus (Text-fig. 2f). Typically, such leaves have been placed in the species *G. adiantoides* (Unger) Heer, originally described from the Pliocene of Italy. Mustoe (2002) applied the extant species name, *G. biloba* to leaves of this type from the Eocene of Republic, McAbee, and Princeton, arguing that there were no obvious differences in form, or venation from the living representatives. Leaves with deeply divided laminae that are similar to younger extant leaves were described from the McAbee site as *G. dissecta* Mustoe (Mustoe 2002). These have not been observed from this flora.

Cupressaceae. Several representatives of this family are present. *Metasequoia occidentalis* (J. S.Newb.) R.W.Chaney

is common in this flora. It can be distinguished from other members of taxodioid Cupressaceae by its opposite leaves (Text-fig. 2e, h). *Metasequoia* is also a common component of other early Eocene compression floras of the Okanagan Highlands and is known in anatomical preservation in the Princeton chert flora of the Allenby Formation [*Metasequoia milleri* G.W.Rothwell et Basinger (Rothwell and Basinger 1979, Basinger 1981, 1984)]. Another taxodioid foliage form could be assignable to *Sequoia* Endl., *Glyptostrobus* Endl. or some other taxodioid genus (Text-fig. 2g, i), but without seed cones it is difficult to tell (although see LePage 2011). One twig bearing pollen cones in alternate organization (Text-fig. 2j) could represent *Sequoia*, *Glyptostrobus* or another genus, but not *Metasquoia* which has oppositely arranged pollen cones. The vegetative leaves are tightly packed, and the flared tips of one specimen suggest poorly preserved remnants of small cones may be present (Text-fig. 2g). Isolated taxodioid seed cones appear to represent *Metasequoia* because they are borne on naked, needleless twigs (Text-fig. 2k). A branchlet with short, tightly imbricate leaves may be assignable to *Chamaecyparis* Spach or another cupressaceous conifer (Text-fig. 2l).

Pinaceae. *Pinus* L. is known from leaf fascicles with 4 or 5 needles (Text-fig. 3a, b), and seeds of the articulate kind typical of the *Diploxylon*-type pine (Text-fig. 3c; Klaus 1989). Other seeds are flattened and have a long wing and less distinct seed body (Text-fig. 3d, e).

Taxaceae. Taxaceous needles have been collected that closely resemble *Amentotaxus* Pilg. (Text-fig. 3f–h). These straplike leaves are ca 8 cm long × 0.4 cm wide and taper at their apical tip. The part-counterpart specimen shows a midvein on the adaxial (upper) surface (Text-fig. 3h) and a pair of stomatal bands impressed on the abaxial (lower) side (Text-fig. 3g). Although the apical tip is missing the taper suggests it is blunt, a feature that distinguishes *Amentotaxus* from *Torreya* Arn. (Text-fig. 3g). Other Cenozoic occurrences of *Amentotaxus* in North America and Europe have been reviewed earlier (Ferguson et al. 1978, Jähnichen 1990).

Angiosperms

Monocots. Three types of monocots have been found (Text-fig. 4a–g). One is an incompletely preserved, broad leaf over 12.5 cm long × 6.5 cm wide with a prominent midrib ca 1 cm wide (Text-fig. 4a, b). Secondary veins arise at about 80° from the midvein and are parallel and spaced ca 0.8 cm apart (Text-fig. 4b). The margin is entire (Text-fig. 4a, at left). Details of higher order venation are not well preserved.

A second type of monocot leaf is incomplete but at least 18 cm long × 0.8 cm wide, elongate and strap-shaped with ca nine major parallel veins with intervening additional thinner veins (Text-fig. 4c–e). Numerous small linear to oval structures 0.5–1.0 mm across with irregular margins occur under the leaf surface (Text-fig. 4e). These linear to oval structures may be the remnants of diaphragm tissues which are preserved at various angles in a fleshy culm. There could also be some damage pattern present. A leaf fragment lying beside this specimen has a similar venation pattern but lacks these structures (Text-fig. 4d). The appearance of
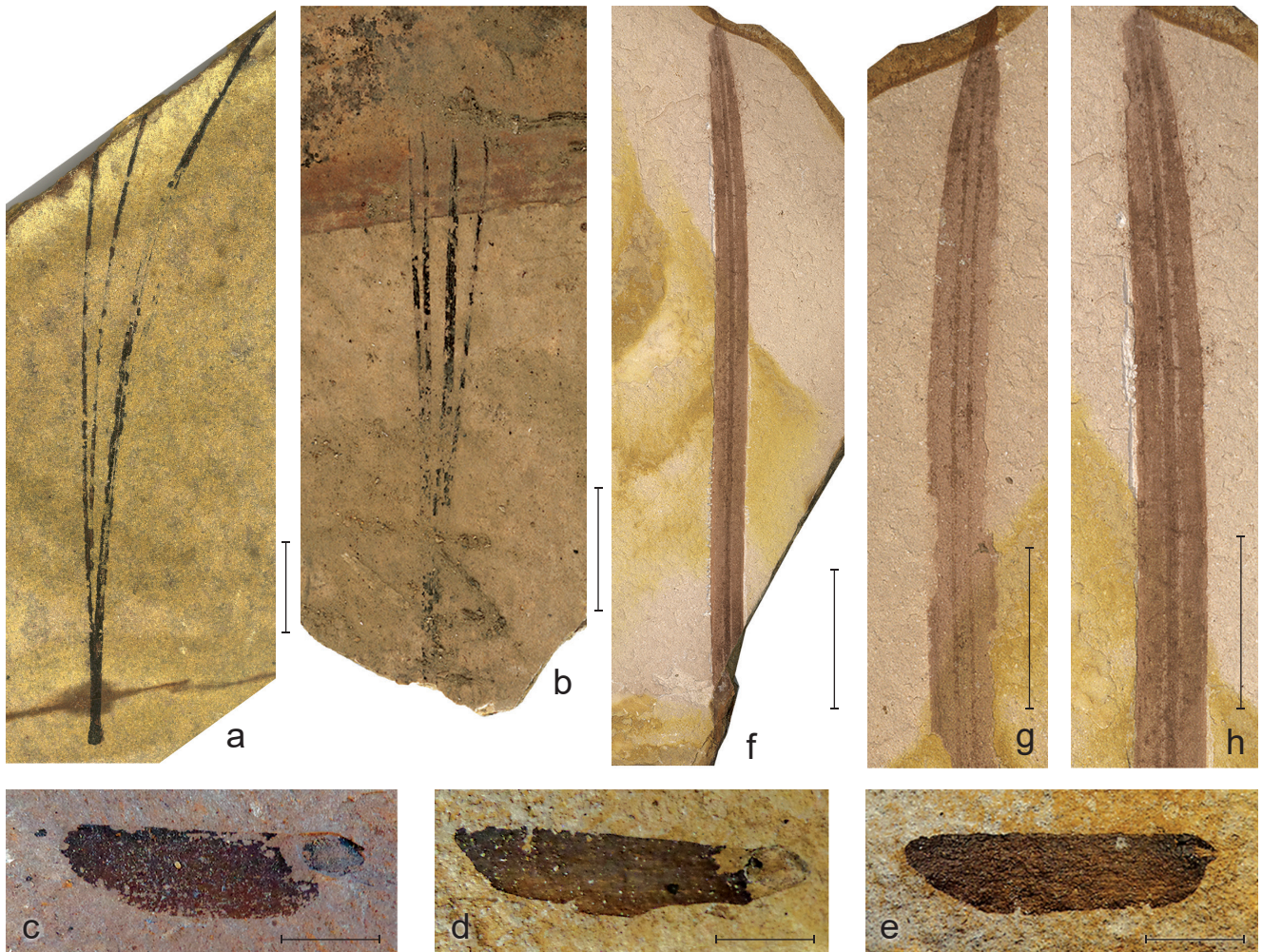
Text-fig. 3. Pinaceae, Taxaceae. a: *Pinus* **needle fascicle with 3 needles, UAPC-ALTA S 25088A. b:** *Pinus* **needle fascicle with at least 4 needles, UAPC-ALTA S 59496. c: Articulate** *Pinus* **seed (section Diploxylon) showing seed body partly detached from wing, BBM-PAL-P000007. d: Winged pinaceous seed with elongate, flattened wing and narrow seed body, BBM-PAL-P000048. e: Another winged pinaceous seed with very narrow seed body, BBM-PAL-P000008. f:** *Amentotaxus* **leaf, UAPC-ALTA S S25086A. g: Higher magnification counterpart of (f) showing abaxial (lower) leaf surface with two parallel stomatal bands and tapered leaf tip S 25086B. h: Higher magnification of specimen in (f) showing adaxial (upper) leaf surface with detail of single midvein. Scale bars: a–e, g, h = 1 cm, f = 2 cm.**

this leaf fragment may be the result of the inner tissues not being preserved. These structures are difficult to interpret with certainty. The third monocot is an incomplete elongate leaf or stem 4.8 cm long × 0.1 mm with parallel venation (Text-fig. 4f, g).

"Dicots"

Lauraceae. The laurel family is represented by large leaves of *Sassafras hespera* (E.W.Berry) J.A.Wolfe et Wehr over 9 cm long and up to 5.5 cm wide (Text-fig. 5a). *Sassafras hespera* leaves are common components of other Okanagan Highlands sites and may be unlobed, bilobed and often "mitten-shaped" with one large and one small lobe as the one figured here, or trilobed. All three leaf morphologies are known on extant *Sassafras albidum* (Nutt.) Nees, even on branches of the same tree (DeSoysa and Kincaid 1991). An additional lauraceous leaf type resembles *Lindera* Thumb. was also found (Text-fig. 5b).
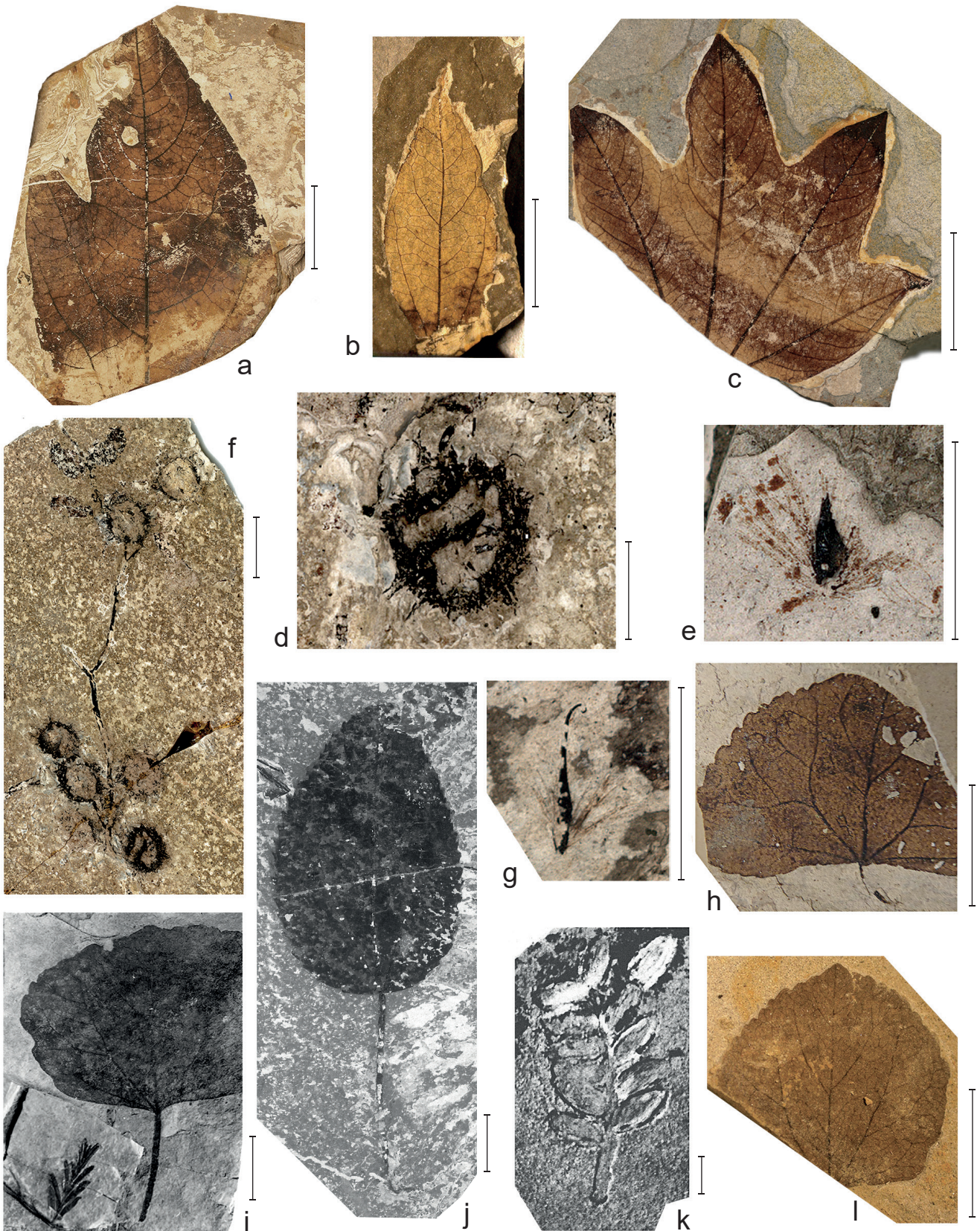
Platanaceae. Leaves of *Macginitiea gracilis* (Lesq.) J.A.Wolfe et Wehr, infructescences of *Macginicarpa* Manchester and individual platanaceous fruitlets occur at

Horsefly (Text-fig. 5c–g). *Macginitiea* leaves (Text-fig. 5c) were first recognized from Horsefly under the name *Aralia notata* Lesq. by Penhallow (1902). This is the most northerly occurrence of the genus yet documented from North America. A *Macginicarpa* infructescence composed of at least five pistillate spherical heads or capitula is borne in the typical raceme-like organization (Text-fig. 5f). *Macginicarpa* capitula have fruitlets clustered in fives (Text-fig. 5d). *Macginitea* leaves co-occur commonly with *Macginicarpa* infructescences at many Paleogene sites in western North America, suggesting they may represent the same biological taxon (Manchester 1986, 2014, Pigg and Stockey 1991). Individual fruitlets with a prominent basal tuft of hairs like those seen in modern *Platanus* L. are also present at Horsefly (Text-fig. 5e, g). These differ from *Macginicarpa* fruitlets which are exclusively glabrous (Manchester 1986).

Cercidiphyllaceae and similar leaves. Several types of rounded to somewhat elongate leaves with actinodromous primary venation and variably toothed or lobed margins with circular glands at the tips of the teeth or lobes, may represent

Text-fig. 4. Monocots. a, b: Large monocot leaf part and counterpart, UAPC-ALTA S 17955A, B. **a:** Wide leaf showing entire margin at left. **b:** Counterpart showing dark wide midrib, and and secondaries parallel to one another, arising at low acute angle. **c–e:** Monocot leaf with parallel venation. **c:** Overview of elongate monocot leaf with parallel veins horizontal and linear to oval structures and smaller leaf fragment of same type lacking them (at lower right), UAPC-ALTA S 59491. **d:** Higher magnification of the smaller fragment with weak cross veins. **e:** Higher magnification of larger specimen with linear to oval structures between parallel veins. **f, g:** Monocot leaf with parallel venation. Fig. (f) shows higher magnification and (g) shows overview, BBM-PAL-P000009. Scale bars: a, b = 5 cm, c = 4 cm, d–f = 1 cm, g = 2 cm.

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Text-fig. 5. Lauraceae, Platanaceae, Cercidiphyllaceae/Trochodendraceae. a: *Sassafras hespera* with 2 lobes, UAPC-ALTA S6556. **b: cf.** *Lindera* leaf. UAPC-ALTA S 67687. **c:** *Macginitiea gracilis*, UAPC-ALTA S 25748. **d:** *Macginicarpa* capitulum showing florets grouped in fives, UAPC-ALTA S 59507. **e, g:** Platanaceous fruitlets with basal tufts of dispersal hairs, UAPC-ALTA S 25748B, S S275238. **f:** *Macginicarpa* infructesence with five attached capitula, UAPC-ALTA S 59507A. **h:** Leaf similar to *Populus* and *Trochodendroides*, BBM-PAL-P000010. **i:** Leaf similar to *Populus* and *Trochodendroides*, UAPC-ALTA S 59516. **j: cf.** *Trochodendroides*, UAPC-ALTA S 59516. **k:** *Jenkinsella* infructesence; Figured in Penhallow 1908, plate 33. **l: cf.** Leaf similar to *Cercidiphyllum* and *Trochodendroides*, BBM-PAL-P000010. Scale bars: a–c, f, h, j, l = 2 cm, d, i, k = 1 cm, e, g = 0.5 cm.
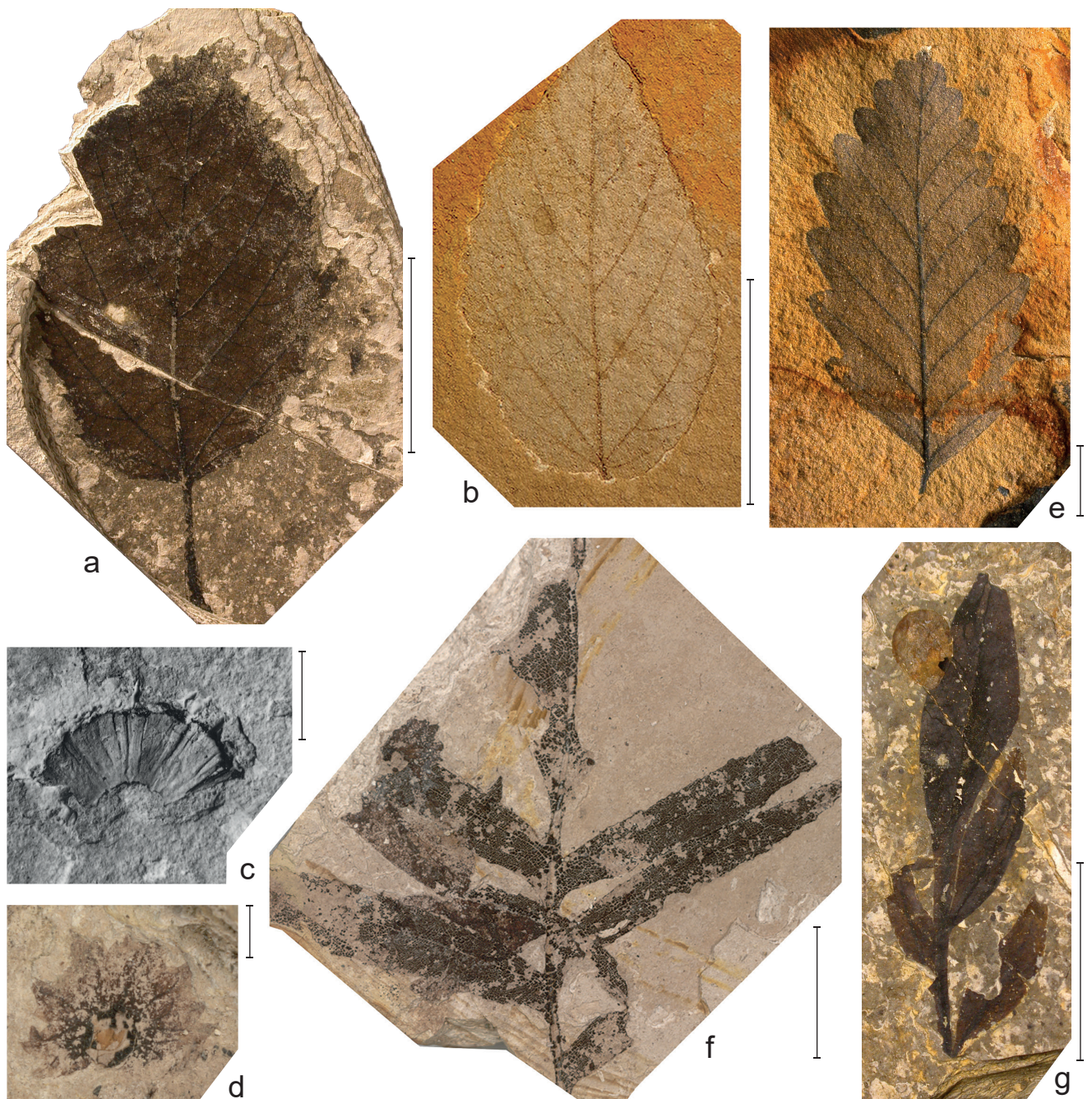
Text-fig. 6. Betulaceae, Fagaceae, Anacardiaceae. a: *Corylites* Sɪᴇʙ., UAPC-ALTA sn. **b:** *Alnus* sp., BBM-PAL-sn. **c:** *Fagopsis* **infructescence, GSC 7586. d:** *Palaeocarpinus barksdalae*, UAPC-ALTA S 59493. **e:** *Fagopsis undulata* **leaf, UAPC-ALTA S 67688. f: cf.** *Schinus* **compound leaf with serrated leaflets basally fused to the rachis, UAPC-ALTA S 24998. g:** *Rhus* **sp., UAPC-ALTA S 67689. Scale bars: a, e = 1 cm, b, f = 2 cm, c, d = 0.3 cm.**

either several taxa or one highly diverse species. Leaves of these types occur in other Okanagan Highlands floras where they have been classified as *Cercidiphyllum* Sɪᴇʙ. et Zᴜᴄᴄ., *Zizyphoides* Sᴇᴡᴀʀᴅ et V.M.Cᴏɴᴡᴀʏ or referred to *Joffrea* P.R.Cʀᴀɴᴇ et Sᴛᴏᴄᴋᴇʏ. *Joffrea speirsii* P.R.Cʀᴀɴᴇ et Sᴛᴏᴄᴋᴇʏ is based on a holotype twig bearing two inflorescences as well as other associated organs from the Paleocene of Alberta, Canada. Its diagnosis includes leaves, inflorescences and infructescences, branching architecture and young seedlings (Crane and Stockey 1985). The diagnosis of *Joffrea* refers to the complete reconstructed plant and therefore should not be used for isolated leaves of the general *Cercidiphyllum* type (Pigg et al., 2001, Dillhoff et al. 2013, DeVore and Pigg 2013).

Recent revision of *Trochodendroides* Gᴏʟᴏᴠɴ. et P.I.Aʟᴇxᴇᴇᴠ includes a variety of leaf forms (Golovneva and Alexeev 2017). This variation is illustrated by a specimen of a branch with three attached leaves each with a different morphology (Manchester 2014: fig. 7.1). An infructescence resembling that of *Joffrea*, previously illustrated from Horsefly by Penhallow (1908: 61, fig. 14; and here reproduced as Text-fig. 5k) was called "*Leguminosites*? *arachioides* Lᴇsǫ."). The infructescences include pod-like fruits similar to *Cercidiphyllum* but are racemes rather than clusters. Such infructescences, commonly found in association with *Trochodendroides*, are assigned to *Jenkinsella* E.Rᴇɪᴅ et M.Cʜᴀɴᴅʟᴇʀ (Text-fig. 5k).

Here we illustrate specimens that could be assignable to *Trochodendroides* (Text fig. 5i, j) or perhaps *Cercidiphyllum* (Text-fig. 5l) or *Populus* L. (Text-fig. 5h, l). Identification of these leaves is further complicated by common leaf dimorphism that occurs in extant *Cercidiphyllum*, *Populus* and leaves from Republic and other Okanagan Highlands sites referred to *Zizyphoides* (Crane et al. 1991, DeVore and Pigg 2013).

Betulaceae. The birch family is represented by leaves of *Corylites* J.S.Gardner and *Alnus* Mill. and fruits of *Palaeocarpinus* P.R.Crane (Crane 1981). *Corylites* leaves are named for their resemblance to those of extant *Corylus* L. (Text-fig. 6a). They are characterized by prominent tertiary veins positioned perpendicular to the secondaries and sometimes form apically pointed chevrons (Text-fig. 6a). In contrast, *Alnus* leaves can be recognized by relatively simple venation lacking chevrons and a slightly undulating margin, with small, widely-spaced teeth (Text-fig. 6b). *Alnus* is the most common dicot leaf form at Republic and it is recorded as present but rarer than *Betula* L. in the One Mile Creek and Thomas Ranch floras (Crane and Stockey 1986, Dillhoff et al. 2013). We have not seen conclusive evidence of *Betula* leaves at Horsefly.

Fruits of the extinct genus *Palaeocarpinus* are rare at Horsefly and are assignable to *Palaeocarpinus barksdalae* Pigg, Manchester et Wehr described from Republic, based on the presence of large wings with well-defined reticulate venation and pointed teeth (Text-fig. 6d; Pigg et al. 2003). Other species previously recognized from the Okanagan Highlands include *P. stonebergae* Pigg, Manchester et Wehr from the Thomas Ranch locality near Princeton, BC, *P. dentata* (Penh.) Pigg, Manchester et Wehr known from Stump Lake, British Columbia, and additional illustrated forms at the Golden Promise Mine near Republic, and Quilchena (Pigg et al. 2003, Correa-Narvaez and Manchester 2021). Specimens from Driftwood Canyon and Horsefly are mentioned previously but not illustrated (Pigg et al. 2003).

Palaeocarpinus is well known throughout the Paleocene of the Northern Hemisphere with 14 species in North America, China and Europe (Manchester et al. 2004, Correa-Narvaez and Manchester 2021). *Palaeocarpinus* survived into the early Eocene with several species in western North America and Kamchatka (Pigg et al. 2003, Correa-Narvaez and Manchester 2021). The co-occurrence at Horsefly of *Palaeocarpinus* with *Corylites* leaves suggests they might represent the same plant. Other Paleocene and Eocene sites show a similar co-occurrence (Sun and Stockey 1992, Manchester and Chen 1996, Manchester and Guo 1996, Manchester et al. 2004). Leaves from these localities are quite different from those associated with the type species *P. laciniata* P.R.Crane (Crane 1981).

Fagaceae. *Fagopsis* Hollick is recognized from both large and small leaves (Text-fig. 6e) and the distinct wedge-like infructescence fragments (Text-fig. 6c) that characterize the genus. This extinct genus was first recorded from Florissant, Colorado (Hollick 1909), where specimens are available showing attachment of flowers and fruits to twigs bearing the leaves (Manchester and Crane 1983). The presence of *Fagopsis* leaves, along with the dispersed fruiting material, indicates that this genus was distributed as far north as Horsefly in the latest early Eocene supplementing the occurrence known from Resner Canyon near Republic (Wolfe and Wehr 1987). Paleocene leaves that were called *Fagopsis groenlandicus* (Heer) J.A.Wolfe have never been found in association with the diagnostic fruits of the genus, and have been reassigned to the foliage genus *Fagopsiphyllum* Manchester (Manchester 1999). True *Fagus* L. is known from the Okanagan Highlands sites at McAbee and Republic (Manchester and Dillhoff 2004); however, neither beech nuts nor leaves have been discovered at Horsefly.

Anacardiaceae. Anacardiaceae is represented by *Rhus* L. (Text-fig. 6g), cf. *Schinus* L. (Text-fig. 6f) and a third leaf type that may be assigned to the family (Text-fig. 9a). A specimen of *Rhus* has pinnately compound leaflets and a winged rachis (Text-fig. 6g). Five species and some putative hybrid leaves of *Rhus* are known from Republic (Flynn et al. 2019). The Horsefly specimen is not easily assignable to any of the five species but is more similar to those from Republic interpreted as putative hybrids. A compound leaf with serrated leaflets basally fused to the rachis resembles those of *Schinus*, the genus that includes the extant Peruvian pepper tree (Text-fig. 6f).

Sapindaceae. This family is represented by fruits of *Acer* L., *Dipteronia* Oliv., *Koelreuteria* Laxm. and several types of leaves. We illustrate pinnately compound leaves assignable (Text-fig. 7a) and potentially assignable (Text-fig. 9b) to Sapindaceae on the basis of leaf architecture, characteristic sinuses and marginal tooth type. Fruits from Republic assigned to *Bohlenia* J.A.Wolfe et Wehr by Wolfe and Wehr (1987) were reassigned to *Dipteronia* by Manchester and McClain (2001), who restricted the name *Bohlenia* to the leaves on which the genus was founded. *Dipteronia* fruits are found both as separate mericarps and complete schizocarps (Text-fig.7 b–c; Manchester and McClain 2001: fig. 10).

Koelreuteria has bladder-like fruits with distinctive reticulately veined valves. The example from Horsefly (Text-fig. 7d) conforms in large size and venation pattern to the fossil species, *K. dilcheri* Q.Wang, Manchester, H.-J. Gregor, S.Shen et Z.Y.Li, which is also known from the Chalk Bluffs and Republic floras (Wang et al. 2013).

Acer fruits are also present but seem to be relatively rare (Text-fig. 7e). The Horsefly specimens are similar to those described from other Okanagan sites (One Mile Creek, Republic) by Wolfe and Tanai (1987). Care must be taken to distinguish *Acer* samaras from those of *Deviacer* Manchester (Text-fig. 7h) as they can be difficult to identify if the scar of mericarp detachment (*Acer*) or rudderlike secondary wing (*Deviacer*) are not clearly preserved.

Polygalaceae. Distinctive winged fruits of the extinct genus *Deviacer* Manchester are recognized by their *Acer* like wing and distinctive style-like protrusion from the fruit body (Text-fig. 7f, h). MacGinitie (1953) first recognized this kind of samara from the Florissant flora and noted that it superficially resembled *Acer* except that their wing was more strongly developed on what appeared to be the ventral rather than the dorsal side and their point of attachment on a thin stalk suggested they were nonschizocarpic. He suggested these fruits resembled *Thouinia* Poit. (Sapindaceae) or *Securidaca* L. (Polygalaceae). Wolfe and Wehr (1987) referred to these fruits informally as "*Acer arcticum*" and considered them a potential
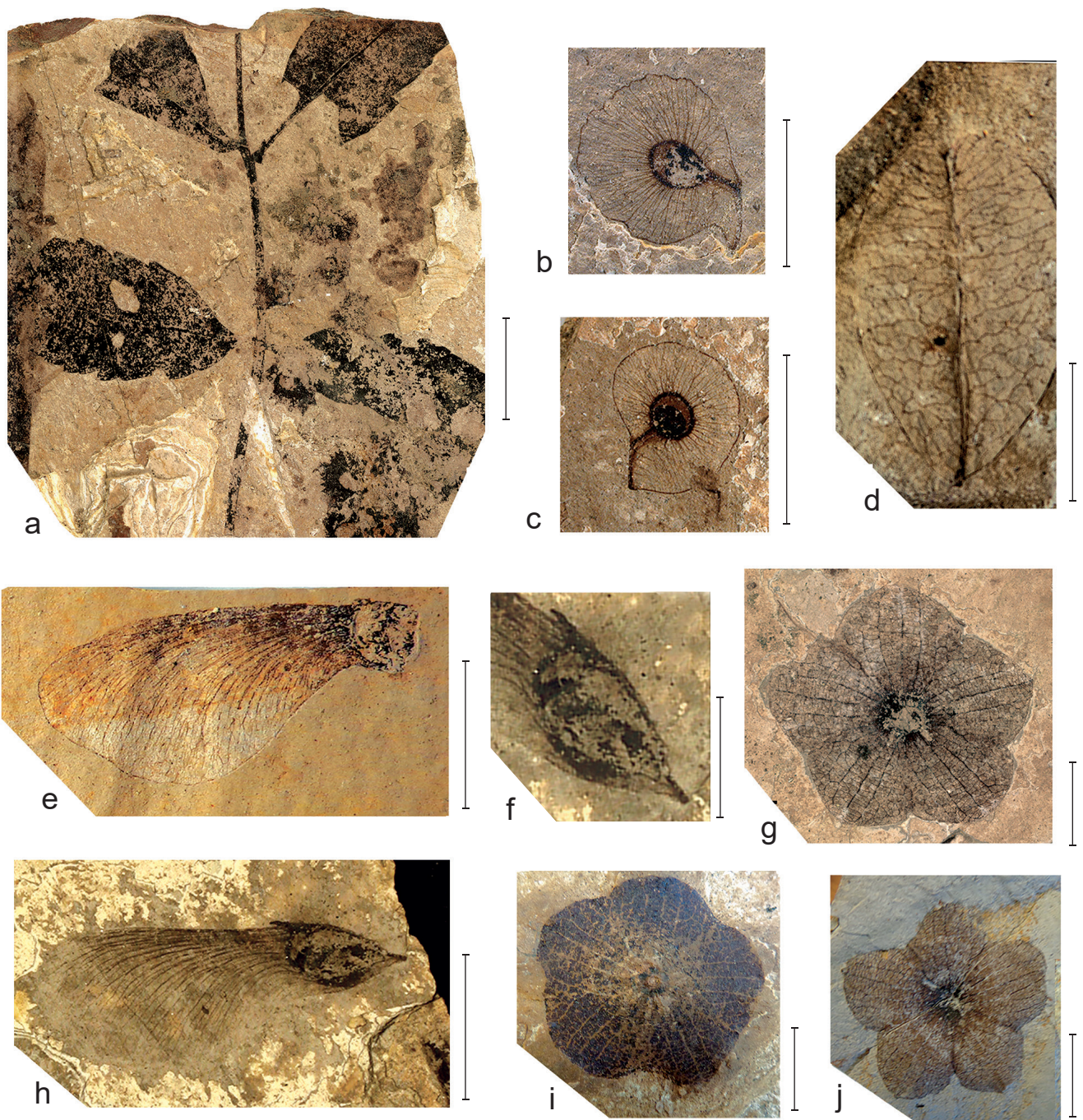
Text-fig. 7. Sapindaceae, Polygalaceae, Malvaceae. a: cf. *Dipteronia* **or** *Koelreuteria* **pinnately compound leaf with serrate leaflets, UAPC-ALTA S 59500. b, c:** *Dipteronia brownii*, **UAPC-ALTA S 59494AB, UAPC-ALTA S 59488. d:** *Koelreuteria dilcheri* **fruit valve, BBM-PAL-P000011. e:** *Acer*, **BBM-PAL-P000012. f: Detail of** *Deviacer* **fruit body from (h). g:** *Florissantia quilchenensis* **calyx, UAPC-ALTA S 26364. h:** *Deviacer wolfei*. **UAPC-ALTA S 67690. i, j:** *Florissantia quilchenensis* **calyces. i: BBM-PAL-P000013. j: BBM-PAL-P000014. Scale bars: a–e, g–j = 1 cm; f = 5 mm.**

evolutionary intermediate between *Acer* and *Dipteronia*. Manchester (1994) named these fruits *Deviacer* based on specimens from the Clarno Formation of Oregon (Text-fig. 7h). Based on fruits of this type with anatomical preservation from the late Paleocene Almont flora of North Dakota Pigg et al. (2008) identified similar but larger late Paleocene fruits to Polygalaceae and named them *Paleosecuridaca* Pigg, DeVore et M.F.Wojc. Myers and Erwin (2015) inferred closer similarity of these extinct fruits to those of *Securidaca* but retained the name *Deviacer* for specimens for which anatomy is not known.

Malvaceae. *Florissantia quilchenensis* (Mathewes et R.C.Brooke) Manchester represents an extinct species of flowers and fruits with a persistent rounded 5-lobed perianth (Manchester 1992). The perianth varies among specimens in the degree of lobation (Text-fig. 7i, j). Specimens with attached stamens are known from Republic. Flowers of the same genus from the late Eocene and early Oligocene of the John Day Formation, Oregon yielded *Tilia*-like pollen and show a pentagonal central fruit body with a style having five stigmatic arms (Manchester 1992). This set of characters is consistent with the currently recognized

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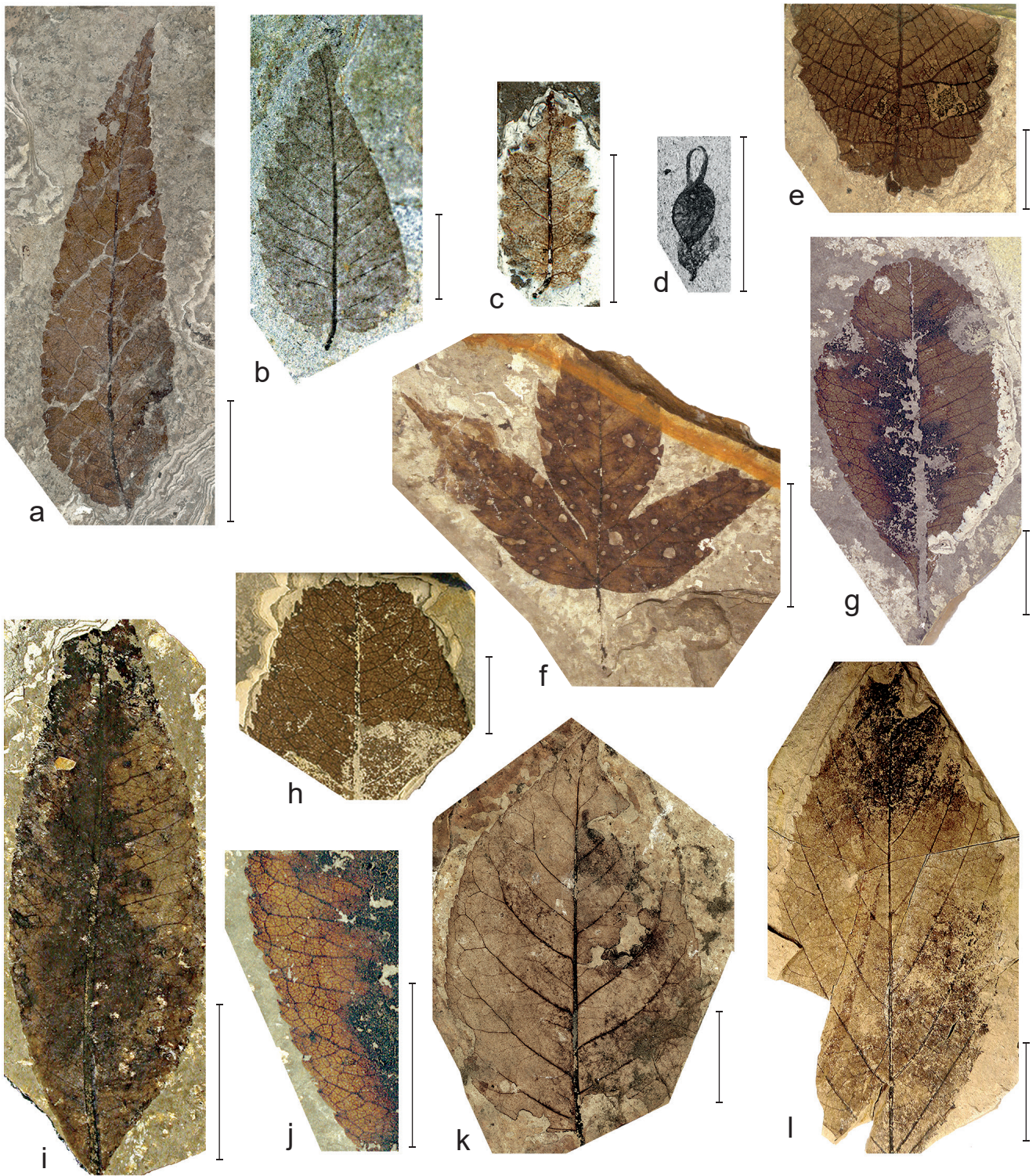
Text-fig. 8. Ulmaceae a–e, Rosaceae f–l. a: *Cedrelospermum*, leaflet missing base but showing simple teeth, UAPC-ALTA S 25748. b: *Ulmus* with prominent teeth, asymmetric base, BBM-PAL-P000015. c: *Ulmus* leaf with prominent teeth, UAPC-ALTA S 59506. d: *Ulmus* fruit, UAPC-ALTA S 6590. e: Basal half of *Ulmus* leaf showing the obtuse teeth with subbasal entry of veins to the teeth, UAPC-ALTA S 59517. f: cf. *Rubus*, UAPC-ALTA S 67691. g. *Prunus* leaf, UAPC-ALTA S 25746. h: cf. *Hesperomeles* UAPC-ALTA S 67692. i: *Photinia pagae*, UAPC-ALTA S 67693. j: cf. *Prunus*, detail from g. k: Rosaceous leaf, UAPC-ALTA S 59501. l: Rosaceae, possibly Kerriae. BBM-PAL-P000047. Scale bars: a, f, i, k, l = 2 cm; b–e, g, h, j = 1 cm.

members of Malvaceae that include the former Tiliaceae, Bombacaceae and Sterculiaceae (because of some similarity to *Fremontodendron* Coville).

Ulmaceae. Leaves and fruits of *Ulmus* and leaves of *Cedrelospermum* Saporta, are recognized from this flora (Text-fig. 8a–e). One of the leaves figured here, which has a simple-toothed margin appears to conform to the extinct ulmaceous genus *Cedrelospermum* (Text-fig. 8a). *Ulmus* leaves are quite variable even within a single species (Text-fig. 8b, c, e; Manchester 1989a), and fruits characteristic of the genus are known at Horsefly (Text-fig. 8d). Denk and Dillhoff (2005) recognized two species of elm fruits and

Text-fig. 9. Miscellaneous leaves. **a: Leaf of Anacardiaceae, UAPC-ALTA S 59513. b: Sapindaceous leaf, BBM-PAL-P000046. c: Twig with compound leaves of *Averrhoites affinis*, UAPC-ALTA S 67694. d, e: *cf. Morus*. Finely serrate leaf with actinodromous venation, prominent agrophic veins and strongly percurrent tertiary veins, UAPC-ALTA S 67695. f: Leaf with strongly apically arched upper pairs of secondary veins and entire margins, UAPC-ALTA S 59504. g: Compound leaf, UAPC-ALTA S 59504A. h: Detail of (g) showing one leaflet. i: Incomplete basal part of a lamina with rounded base and entire margin, UAPC-ALTA S 6565. j: Compound leaf with leaflets sessile on a stout rachis, UAPC-ALTA sn. Scale bars: a, c, d, i = 2 cm, b, e–h, j = 1 cm.**

foliage based on specimens from other Okanagan localities, especially McAbee. Although *Cedrelospermum* fruits have not been found at Horsefly, the samaras have been found attached to twigs bearing leaves similar to that of Text-fig. 8a, from the Green River and Florissant formations (Manchester 1989b).

Rosaceae. The rose family is well represented in the Okanagan Highlands floras and many taxa have their
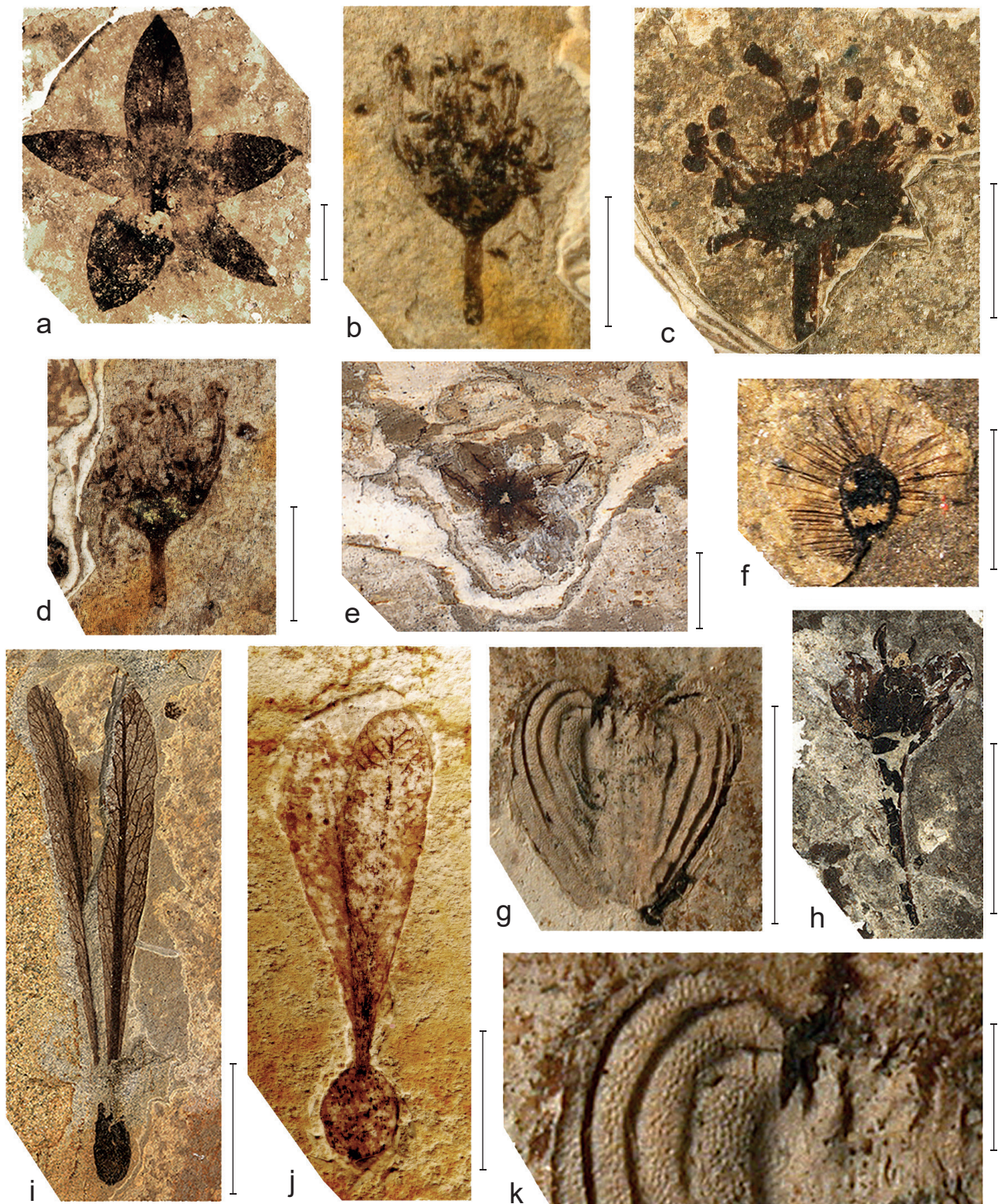
Text-fig. 10. Flowers and fruits. a: Pentamerous flower from top view, UAPC-ALTA S 67696. b, d: Part and counterpart of a flower with many stamens, type 1 UAPC-ALTA S 6560AB. c: Flower with many stamens, type 2, UAPC-ALTA S 26359. e: Small radially symmetric flower with pinnate venation in each sepal. UAPC-ALTA S 25356. f: *Pteroheterochrosperma horseflyensis*, UAPC-ALTA S 59494B. g, k: Fruit showing arched longitudinal ribs and and punctate surface, UAPC-ALTA S 26355A. h: Small flower UAPC-ALTA 26360. i: *Lagokarpos lacustris*, UAPC-ALTA S 59498B. j: *Lagokarpos lacustris*, RBCM.EH2009.023.0003. Scale bars: a–d, g, h = 0.5 cm; e, f, k =0.2 cm; i, j = 1 cm.

oldest known occurrence at these localities. DeVore and Pigg (2007) reviewed the fossil record of Rosaceae with an emphasis on the Okanagan Highlands. This family is represented in the Horsefly flora by *Rubus* L. (Text-fig. 8f).

Prunus L. (Text-fig. 8g, j), cf. *Hesperomeles* LINDL. (Text-fig. 8h), *Photinia pageae* J.A.WOLFE et WEHR (Text-fig. 8i), and possibly additional genera (Wolfe and Wehr 1987, 1988, DeVore and Pigg 2007). Text-fig. 8k depicts a rosaceous leaf

with prominent secondaries, marginal loops and a gently toothed margin. The leaf in Text-fig. 8l resembles the tribe Kerrieae based on the distinctive tooth type found in this group. *Neviusia* Gray leaves were originally described from One Mile Creek (DeVore et al. 2004) and both *Neviusia* and *Kerria* DC have been identified from Republic (DeVore and Pigg, pers. obs. 2000).

Leaves of uncertain affinity. Several additional leaves of unknown affinities are present at Horsefly. The first (Text-fig. 9a) is a leaf with the characteristic morphology, venation and marginal teeth of Anacardiaceae. A pinnately compound leaf with prominent, entire-margined lobes having strong primary veins and subopposite secondaries has the general leaf architecture, sinuses and marginal tooth type of some sapindaceous leaves (Text-fig. 9b). *Averrhoites* L.Hickey (Text-fig. 9c) is characterized by imparapinnately compound leaves with asymmetrical entire-margined, pinnately-veined leaflets. This leaf type might correspond to the same extinct plant that produced flowers of *Pistillipollianthus* Stockey et Manchester. Both also occur together at several localities in the Paleocene of western North America (Manchester 2014, Scott Wing, pers. comm. 2022). Text-fig. 9d, e shows a leaf that resembles extant *Morus* L. (Moraceae). This leaf has a finely serrate margin, actinodromous venation, prominent agrophic veins and strongly percurrent tertiary veins.

Entire-margined leaves of uncertain affinity were compared with *Cornus* L. (Text-fig. 9f) because they resemble modern dogwood leaves by the strongly apically arched upper pairs of secondary veins and regularly spaced percurrent tertiary veins. However, trichomes diagnostic of *Cornus* which can be observed at high magnification in impression fossils (Manchester et al. 2009) were not seen on this specimen. This leaf is similar in architecture to some of Melastomataceae (e.g., *Miconia brenesii* Standl) and Urticaceae (*Pilea* Lindl.).

Text-fig. 9g, h is a compound leaf with alternately arranged leaflets that are spaced fairly far apart and decurrent along their attachment to the rachis. The leaflets have strong midveins and are elongate with craspedodromous secondary veins, well preserved higher orders of venation and prominent sharp, marginal teeth (Text-fig. 9h). Text-fig. 9i shows a partially preserved rounded leaf with an entire margin. Text-fig. 9j is a pinnately compound leaf with a series of subopposite leaflets that appear to be sessile on a stout rachis. The leaf is charcoalified such that details of venation are not clear.

Flowers and fruits. Several angiosperm reproductive structures are known from Horsefly. The previously described *Pistillipollianthus wilsonii* Stockey et Manchester is an actinomorphic flower containing the distinctive *Pistillipollenites macgregori* Rouse pollen. This flower is 2.1 cm in diameter with six sepals and six stamens and a probably superior ovary (Stockey and Manchester 1988). *Pistillipollenites* Rouse pollen is triporate and covered with distinctive gemmate exine, nannoverucae and ubisch bodies. This widely dispersed pollen type is known also to occur in a flower from the Eocene of Texas (Crepet and Daghlian 1981) that was compared with Gentianaceae. The Texas flower is dissimilar to the Horsefly one in numerous features, suggesting convergence of morphology of this pollen type. In the present study we illustrate a radially symmetric,

pentamerous flower preserved in top view (Text-fig. 10a). This flower somewhat resembles *Pistillipollianthus* except in having flower parts in 5s rather than in 6s as is characteristic of the published specimens (Stockey and Manchester 1988). It may be a distinct taxon. A much smaller, radially symmetric, pentamerous flower of unknown affinities is illustrated in Text-fig. 10e. It is distinctive in possessing sepals with midveins and pinnate secondary veins.

Several flowers bearing numerous stamens are known (e.g., Text-fig. 10b). These flowers have an expanded receptacle that could be referred to as a hypanthium, which is a characteristic feature of Rosaceae. An additional, small flower is illustrated in Text-fig. 10h.

The small winged fruit or seed with radiating striations illustrated in Text-fig. 10f was designated as *Ulmus minuta* Goepp. (Penhallow 1908) and illustrated as a "burr" from Republic by Pigg and Wehr (2002). Disseminules of this type have been designated as *Pteroheterochrosperma horseflyensis* (Smith et al. 2023). Another interesting disseminule is characterized by a hard central body with arched longitudinal ridges and a punctate surface (Text-fig.10g, k) that resembles two mericarps of a schizocarpic fruit that may belong to Apiaceae.

Lagokarpos lacustris, the so-called "rabbit ear fruit" was described from lacustrine deposits at several Eocene sites in western North America (McMurran and Manchester 2010). This distinctive fruit (Text-fig. 10i, j;) has two elongate wings with pinnate venation attached to an elliptical to globose fruit. Its affinities are unknown, but the genus has also been recognized from the Eocene of Germany and Tibet (Tang et al. 2019).

Discussion

Observations on the Horsefly flora

The Horsefly flora supported at least one moss, two filicalean ferns, *Azolla*, several conifers, *Ginkgo*, several monocots and approximately 35 "dicots." Well known plants that occur commonly at other Okanagan Highlands sites include the following: *Ginkgo*, *Metasequoia*, *Pinus*, *Sassafras*, *Macginitiea*, *Macginicarpa*, *Alnus*, *Corylites*, *Palaeocarpinus*, *Fagopsis*, *Koelreuteria*, *Dipteronia*, *Acer*, *Deviacer*, *Florissantia*, *Cedrelospermum*, *Ulmus*, *Photinia* and *Prunus*. The bryophyte is a moss described from a single specimen as *Aulacomnium* (Janssens et al. 1979). It would be interesting to find more information about bryophytes especially with the recent discovery of bryophytes from other fossil floras (e.g., Bippus et al. 2022).

Platanaceae is recognized by the presence of *Macginitiea* and *Macginicarpa*, taxa expected in Okanagan Highlands floras. Fruitlets with dispersal hairs diagnostic of *Platanus*, are known from the middle and late Eocene of Oregon including in the middle Eocene Cherry Creek flora (Manchester 2000, Soltis et al. 2018, Manchester, pers. observ. 2023), as well as Horsefly (Text-fig. 5e, g). It is interesting that *Betula* does not appear to be present because it is common at other Okanagan Highlands localities. The Horsefly flora also includes the northernmost occurrence of the extinct fagaceous genus *Fagopsis*. Although leaves

referred to *Cercidiphyllum*, *Populus* and *Trochodendroides* are known from numerous Paleogene localities it is sometimes difficult to distinguish these genera with certainty. The co-occurrence here and at other localities of *Jenkinsella* and *Trochodendroides* supports the presence of this leaf type at Horsefly. Beyond the identifications provided here, we recognize additional leaves probably belonging to Rosaceae, Sapindaceae and Anacardiaceae that require additional study to classify to genus.

Perhaps the best known of the reproductive structures from Horsefly is the flower *Pistillipollianthus* described by Stockey and Manchester (1988) with its highly distinctive pollen *Pistillipollenites*. The same kind of flower (Crane et al. 1990: text-fig. 25k) and pollen (Zetter et al. 2011: pl. 9, figs 14–18) are known from the Paleocene of Almont, North Dakota. Several other reproductive structures that may add to our understanding of the biodiversity of the Horsefly flora are yet to be studied in detail. These include a small seed (Text-fig. 10f) recently described as *Pteroheterochrosperma horseflyensis* (Smith et al. 2023) that is commonly found at Republic (Pigg and Wehr 2001) and a flower with a distinctive papillate surface that may be assignable to Apiaceae (Text-fig. 10g, k). The biwinged fruit *Lagokarpos* (Text-fig. 10i, j) is uncertain as to familial affinity. The floristic content of the Horsefly sediments provides another piece of the puzzle needed to understand the paleoecology of the Horsefly, along with other Okanagan Highlands floras.

Biogeographic considerations

As indicated above the Horsefly flora bears many elements in common with other floras of the Okanagan Highlands indicating similar environmental conditions over a broad noncoastal area of northwestern North America. Most of these genera are deciduous today and shared with the Paleogene of Asia, suggesting likelihood of a Beringial connection (e.g., Tang et al. 2019). Others were circumboreal, found in the Paleogene of Europe as well as Asia, e.g., *Devicer* (from Eocene Fur flora of Denmark), and *Palaeocarpinus* from the Paleocene of the UK and France. *Florissantia* is known from the late Eocene Amgu flora of far Eastern Russia (Manchester 1999) and *Dipteronia* fruits are known from the Oligocene of China. Although *Fagopsis*, *Macginitiea*, and *Sassafras* appear to have been endemic to western North America during the Paleogene, the shared genera demonstrate probable floristic exchange between northwestern North America and northeastern China during the early Paleogene.

The flora at Horsefly appears to be less diverse than those known from McAbee and Republic. However the sheer intensity of public collecting at McAbee and Republic has generated more specimens and accordingly more of the rare items. Our current work shows the potential for Horsefly flora to be similarly informative if more intensive field work will be undertaken in the future.

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