



FOSSIL FLORA AND PALAEOCLIMATE OF THE UPPER CRETACEOUS HORSESHOE CANYON FORMATION, HORSETHIEF MEMBER, AT MORRIN BRIDGE, ALBERTA, CANADA

CHRISTOPHER K. WEST^{1,*}, KATHARINA HALBWIDL², LEYLA J. SEYFULLAH², TAMMO REICHGELT³, DAVID R. GREENWOOD⁴

¹ Royal Tyrrell Museum of Palaeontology, PO Box 7500, Drumheller, Alberta T0J 0Y0, Canada; e-mail: christopher.west@gov.ab.ca.

² Department of Palaeontology, University of Vienna, Josef-Holaubek-Platz 2, 1090 Vienna, Austria; emails: katharina.halbwidl@univie.ac.at, leyla.seyfullah@univie.ac.at.

³ Department of Earth Sciences, University of Connecticut, Storrs, CT 06269, USA; email: tammo.reichgelt@uconn.edu.

⁴ Biology Dept., Brandon University, 270-18th Street, Brandon, Manitoba, R7A 6A9, Canada; email: greenwoodd@brandonu.ca.

* corresponding author

West, C. K., Halbwidl, K., Seyfullah, L. J., Reichgelt, T., Greenwood, D. R. (2026): Fossil flora and palaeoclimate of the Upper Cretaceous Horseshoe Canyon Formation, Horsethief Member, at Morrin Bridge, Alberta, Canada. – Fossil Imprint, 82(1): 131–170, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).

Abstract: The Horseshoe Canyon Formation in southern Alberta, Canada, preserves abundant plant fossils from the upper Campanian to upper Maastrichtian. However, studies describing the macroflora are taxonomically out of date, and limited work has been done to utilise the flora for palaeoclimatic reconstruction. Fifty-eight plant taxa are documented from the Morrin Bridge locality within the lower Maastrichtian Horsethief Member of the Horseshoe Canyon Formation. The assemblage is composed of gymnosperms, including diverse Cupressaceae, cycadophytes, and ginkgophytes, with rare ferns, and a relatively diverse suite of angiosperms, including dicot leaves of Platanaceae, Cercidiphyllaceae, Trochodendraceae, Betulaceae, and two monocots. Leaf physiognomy-based palaeoclimate reconstructions suggest a mean annual temperature of 12.4 ± 2.7 °C, warmest quarter temperature of 20.0 ± 2.5 °C, and coldest quarter temperature of 3.8 ± 3.2 °C, a mean annual precipitation of 1,282 (–405/+585) mm·yr^{–1}, relative humidity of 81.8 ± 9.3 %, and wettest month and driest month precipitation was 155 (–57/+90) mm and 71 (–39/+90) mm, respectively. This indicates a warm-temperate, humid environment, with modest temperature seasonality and minor precipitation seasonality. These results align with palaeosol data and sedimentological indicators of saturated floodplain conditions transitioning to more fluvial systems.

Key words: Western Canada, palaeobotany, macroflora, Maastrichtian, palaeoclimate

Received: August 27, 2025 | Accepted: February 25, 2026 | Issued: October 7, 2026

Introduction

Upper Cretaceous fossil floras provide an opportunity to understand vegetation character and dynamics at a crucial time in plant evolutionary history. Today, and for most of the Cenozoic, angiosperms have dominated terrestrial vegetation, with dominant coniferous tree cover in boreal and alpine forests the major exceptions. Mesozoic vegetation, however, was dominated by gymnosperms and other non-angiosperm groups. The character and composition of terrestrial vegetation underwent a global transformation, beginning in the Albian, due to the rapid diversification, and increasing importance, of angiosperms (Wolfe and Upchurch Jr. 1986, 1987, Lupia et al. 1999, Herendeen et al. 2017, Kalyaniuk et al. 2023). In western North America, angiosperms diversified rapidly during the Cretaceous, but gymnosperms and pteridophytes

often remained abundant, or the dominant, components of many ecosystems until the K-Pg extinction event (e.g., Spicer 1989, Wilf et al. 2003, 2023, Wilf and Johnson 2004).

A rich succession of fossil floras of the Western Interior of the United States has been extensively studied and offers insights into the Late Cretaceous rise to dominance of angiosperms in terrestrial ecosystems (Dorf 1942, Johnson et al. 1989, Johnson 1992, 2002, Wilf and Johnson 2004). Comparatively, coevally aged floras from Western Canada have seen far less attention. This is not to say there has been no research into the Late Cretaceous vegetation of Western Canada, as there are numerous papers focusing on single taxa (e.g., Brink et al. 2009, Klymiuk et al. 2015, Stockey et al. 2020, Edmonds et al. 2022, Greenwood et al. 2022, Rothwell and Stockey 2022). Some recent palaeoenvironment focused studies have been based on Canadian Upper Cretaceous macrofloras, but

these have either provided cursory examinations of uppermost Maastrichtian floral assemblages from Saskatchewan (e.g., McIver 2002, Bamforth et al. 2014; Text-fig. 1), or Cenomanian macrofloras from eastern Canada (e.g., Demers-Potvin and Larsson 2019), or Turonian to Campanian floras on rafted terranes of coastal British Columbia (e.g., Pearson and Hebda 2006, Jonsson and Hebda 2015). Studies that review the entirety of Upper Cretaceous fossil floras from Western Canada are rare, the most recent of which come from the 1940s and 1950s (Bell 1949, 1956). Thus, there is a need to review and describe the many Upper Cretaceous fossil floras from Western Canada, especially the rich fossil floras of Alberta.

The upper Campanian–upper Maastrichtian Horseshoe Canyon Formation is a mostly terrestrial to marginally marine unit exposed extensively across southern and central Alberta containing clastic sediments and horizontally extensive cyclic coal units (Eberth and Braman 2012). It records a complex interplay of coastal plain, fluvial, and estuarine environments influenced by both tectonics and eustatic sea-level changes (Eberth and Braman 2012 and references therein). The formation is well known for its diverse vertebrate fossil record, particularly dinosaurs (e.g., Eberth et al. 2013, Bell and Campione 2014, Eberth and Bell 2014, Evans et al. 2015), but also preserves abundant plant macrofossils (e.g., Bell 1949, Aulenback and Braman 1991, Serbet and Stockey 1991, McIver and Aulenback 1994, Aulenback and LePage 1998, Serbet and Rothwell 1999, 2003, 2006, 2025, Eberth and Braman 2012, Serbet et al. 2013). Despite this prior work, the Horseshoe Canyon Formation's fossil macroflora remains understudied compared to its faunal assemblages. In general, the macrofossil collections from this formation have received only cursory attention or were documented in a mid 20th-century monograph by Bell (1949), with the exception of the three-dimensionally preserved mesoflora which has seen relatively extensive study (Aulenback and Braman 1991, Serbet and Stockey 1991, McIver and Aulenback 1994, Aulenback and LePage 1998, Serbet and Rothwell 1999, 2003, 2006, 2025, Serbet et al. 2013; Halbwidl et al. 2026). As such, the Horseshoe Canyon Formation presents a valuable yet underutilised opportunity to reconstruct Late Cretaceous vegetation in Western Canada and to explore floral diversity, palaeoecology, and regional palaeoclimate at a time in the few million years prior to the end-Cretaceous mass extinction.

One such locality offering potential for palaeobotanical analysis is found near Morrin Bridge in central Alberta (Text-fig. 1), where exposures of the uppermost Campanian–lower Maastrichtian Horsethief Member of the Horseshoe Canyon Formation have yielded a diverse assemblage of fossil leaves and plant reproductive organs. By specimen numbers, the fossil flora collection is dominated by gymnosperms, including conifers, ginkgophytes, and cycadophytes, but also includes multiple angiosperm leaf taxa and rare fern and horsetail material. This pattern replicates the limited published palynological data, with Eberth and Braman (2012) noting high gymnosperm pollen counts relative to angiosperms (61.2 % vs. 16.7 %) for the Horsethief Member. The fossil flora of the Horsethief Member has received limited systematic attention, with the Morrin Bridge locality offering a valuable opportunity to document the composition and structure of Late Cretaceous – that is, early Maastrichtian – plant communities

in Alberta, at relatively high palaeolatitudes (~60 °N; Quinney et al. 2013 and references therein).

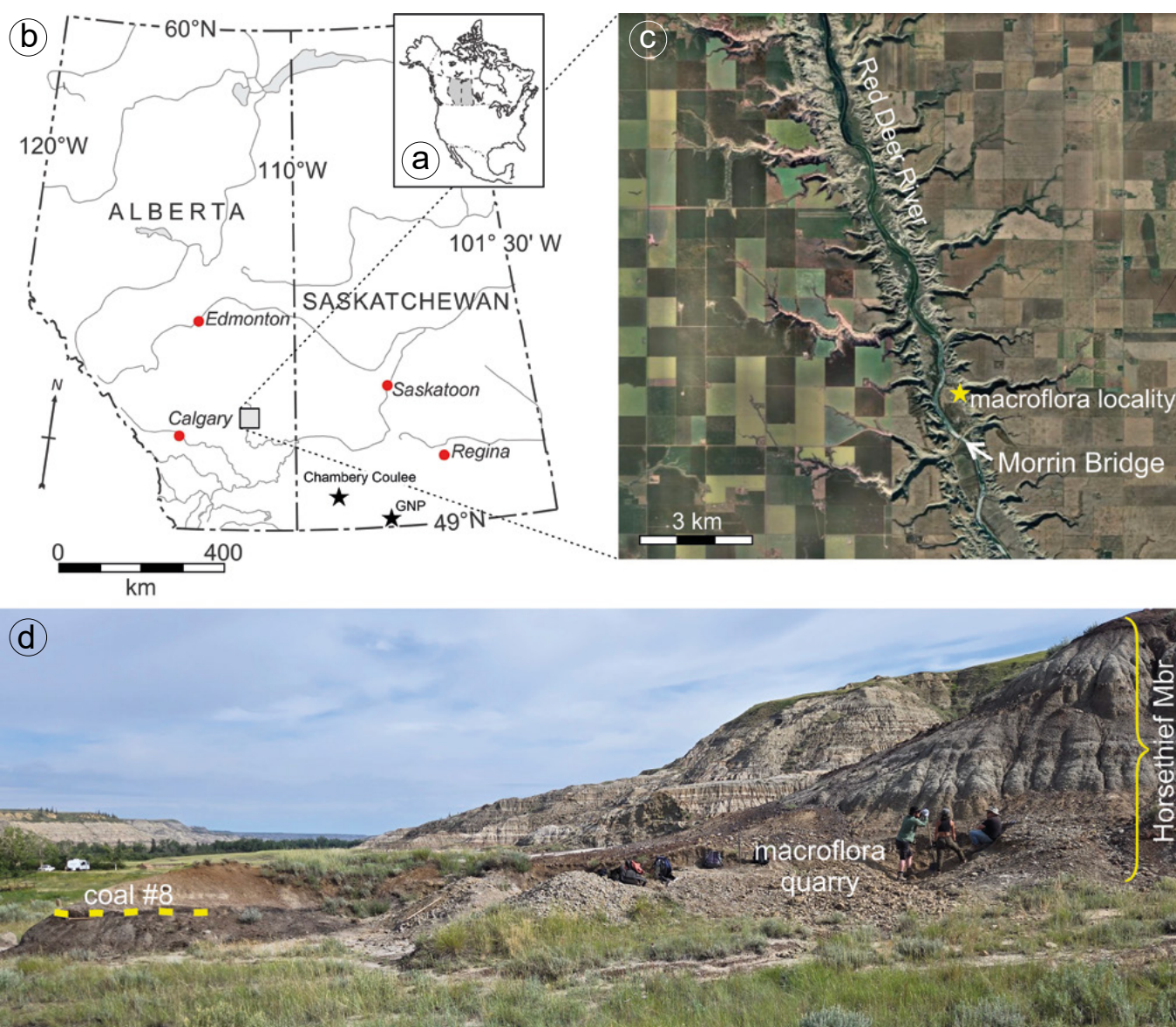
Here, we provide a survey and description of the lower Maastrichtian fossil flora from the Morrin Bridge fossil locality, found near the Morrin Bridge townsite in Alberta, Canada (Text-fig. 1). We discuss the taxonomic composition and diversity of the flora and compare it to previously reported Upper Cretaceous megaflores of the Western Interior. In addition, we provide quantitative palaeoclimate reconstructions based on leaf physiognomy methods, similar to some prior studies based on other Canadian Upper Cretaceous macrofloras (e.g., Pearson and Hebda 2006, Bamforth et al. 2014, Demers-Potvin and Larsson 2019). Documenting and describing the fossil flora of the Horseshoe Canyon Formation represents an initial step toward a more comprehensive understanding of its palaeobotanical record.

Materials and methods

Stratigraphy and age

The collection presented in this report was made from a natural exposure of fluvial sediments of the Horsethief Member sitting just above coal seam number 8 in the upper Campanian to upper Maastrichtian Horseshoe Canyon Formation succession (Eberth and Braman 2012; Text-fig. 1). The Horseshoe Canyon Formation (HCF) is an Upper Cretaceous geological unit located in Alberta, Canada and is part of the Edmonton Group. Seven members (i.e., Strathmore, Drumheller, Horsethief, Morrin, Tolman, Carbon, and Whitemud) make up the formation (Eberth and Braman 2012, Greenwood et al. 2022). The HCF is composed of paralic to nonmarine deposits that reflect a range of coastal plain environments, including alluvial, estuarine, and brackish-water settings. Lithologies are highly variable but commonly include interbedded and inter-lensed sandstones, siltstones, mudstones, carbonaceous shales, and coals (Eberth and Braman 2012). Bentonite is widespread throughout the formation, with some units containing abundant volcanogenic minerals, including biotite and feldspar, suitable for radiometric dating (Eberth and Braman 2012, Eberth and Kamo 2020). The lower contact of the HCF is gradational with the shales of the underlying Campanian Bearpaw Formation, whereas the HCF is unconformably overlain by the Maastrichtian Battle Formation (Eberth and Braman 2012, Eberth and Kamo 2020, Greenwood et al. 2022). Regionally, the HCF correlates with portions of the Wapiti Formation in northern Alberta, the Brazeau Formation in the south-central foothills, and the St. Mary River and Blood Reserve formations in southern Alberta (see fig. 2 in Greenwood et al. 2022).

Several radiometric ages help constrain the deposition of the HCF, which ranges from approximately 73.1 to 68 Ma based on U-Pb dating by Eberth and Kamo (2020). Most relevant to this study is the Trentham Road Bentonite (TRB), located within the number 8 coal zone of the upper Horsethief Member, which yields an age of 71.83 ± 0.44 Ma (Eberth and Kamo 2020). The Morrin Bridge fossil flora was collected from strata just above the number 8 coal within



Text-fig. 1. Details of the fossil locality. a: Map of North America, b: map of Alberta and Saskatchewan showing Morrin Bridge and other Upper Cretaceous macroflora localities mentioned in the text, c: satellite view of Morrin Bridge and fossil locality, d: view of the fossil site showing the lithostratigraphy. Map (b) modified from Greenwood et al. 2022: fig. 1.

the Horsethief Member. The Horsethief Member has been interpreted as having formed under warm, humid coastal to alluvial plain conditions during a relatively warm interval of the Late Cretaceous (Eberth and Kamo 2020). It comprises a coal-rich succession of alluvial-to-paralic and peat swamp environments that suggest a warm and humid palaeoclimate during the latest Campanian to early Maastrichtian (~72–70 Ma) with faunal and palynological evidence suggesting warmer conditions during Horsethief time than higher in the local HCF succession (Eberth and Braman 2012, Eberth and Kamo 2020). The boundary between the Horsethief Member and the overlying Morrin Member is positioned at the top of the number 9 coal zone and corresponds to a marked reduction in grain size and palaeochannel dimensions, interpreted as a climatic transition from warm and humid to cooler and drier conditions and possibly tectonic controls on sediment supply (Eberth and Braman 2012). A significant faunal turnover in megaherbivore dinosaurs and a palynostratigraphic shift also occur at this level (Eberth et al. 2013, Braman 2018).

The Morrin Bridge fossil locality and macroflora

The Morrin Bridge fossil locality is near the Starland Recreation Area and approximately 11 km west from the Morrin townsite (Text-fig. 1). The fossils were sampled from a quarry dug into the side of a natural exposure from approximately 60 cm of strata between the number 8 and number 9 coal seams which marks the top of the Horsethief Member of the HCF (see Eberth and Braman 2012). Fossils were quarried using hand tools and were collected over numerous field seasons from the 1990s until the present by staff and volunteers of the Royal Tyrrell Museum of Palaeontology (TMP), with fossil plant material recovered as impressions and compressions. Specimens were photographed with a Nikon DSLR 5300 digital camera and illuminated using a pair of incandescent lights adjusted to appropriate angles to highlight venation detail. Specimens were deposited with TMP as part of the palaeobotany collection and are cited using TMP accession numbers. For fossil plant names we adopt the

taxonomic and nomenclatural framework provided by the International Fossil Plants Index (IFPNI 2014 onwards).

Plant fossil terminology

Terminology for conifer ovuliferous cones is specialised and can be complex. Ovuliferous cones consist of individual reproductive units. These units are variously referred to either as “bract-scale complex” or “ovuliferous complex” (Escapa et al. 2016). Escapa et al. (2016) argue that the term “bract-scale complex” implies a specific configuration of reproductive units of an ovuliferous cone based on homology hypotheses. These homology relationships between cones of different genera of the Cupressaceae are not resolved, rendering the use of the term “bract-scale complex” potentially problematic (Escapa et al. 2008). The type of preservation of the fossils described in this study does not allow an appraisal of the structures and homology hypotheses underlying the term “bract-scale complex.” Thus, we follow Escapa et al. (2016) and use the more general term “ovuliferous complex”, which describes any ovule-bearing structure of coniferous ovulate cones (see Escapa et al. 2008). We differentiate between foliate, pseudopeltate, peltate, and valvate ovuliferous complexes, following Andruchow-Colombo et al. (2022). The length measurement of decurrent leaves of conifers always refers to the free part of the leaf only. The width measurement denotes the maximum width. In falcate and awl-shaped leaves, we measured the maximum length between the abaxial keel of the leaf and the leaf margin to denote the width of the leaves. For dorsiventrally flattened leaves, the width was measured from margin to margin.

Terminology for the description of angiosperm leaf architecture follows Ellis et al. (2009), which provides a standardised framework for characterising leaf morphology in both extant and fossil-taxa. This system includes detailed criteria for describing leaf shape, size, base and apex form, margin type, venation architecture (e.g., pinnate, palmate, craspedodromous, brochidodromous), and higher-order vein patterns. Use of this terminology ensures consistency and facilitates comparisons across palaeobotanical studies.

Palaeoclimate reconstruction

Plants are constantly interacting with their surrounding environment and adapting to changes, such as those resulting from climate. Consequently, plants are excellent proxies for climate. The leaves of woody broadleaf dicot trees are especially suited for this purpose, as they have a relatively complex leaf architecture that is optimised for photosynthesis, and this architecture is preserved in leaf impressions and compressions. The physiognomy of dicot leaves is typically governed, to some extent, by adapting to the local climate and is thus an expression of that climate. Ancient broadleaf dicot trees undoubtedly also needed to balance photosynthetic efficiency with optimal leaf morphology, and as such, fossil leaf physiognomy can be used to retrodict past climates. The three primary physiognomic methods for palaeoclimate reconstruction are Leaf Area Analysis (LAA), Leaf Margin

Analysis (LMA), and the Climate Leaf Analysis Multivariate Program (CLAMP). These methods are taxon-independent approaches that reconstruct climate from leaf form rather than phylogenetic relationships. A sample size of approximately 20 distinct leaf morphotypes or taxa is typically considered the minimum for robust physiognomic climate reconstructions (Yang et al. 2011, 2015), and the Morrin Bridge flora surpasses this requirement.

LMA is based on the correlation between the proportion of leaves with untoothed margins, or leaf margin proportion (LMP), and mean annual temperature (MAT). Higher LMP within a flora typically suggests warmer climatic conditions. Equation 1 represents the classic LMA regression (Wing and Greenwood 1993). The standard error for MAT estimated by Equation 1 is calculated using the number of leaf taxa identified within the fossil assemblage (Equation 2; Wilf 1997), where r denotes the number of leaf taxa.

$$\text{MAT} = 1.141 + (30.6 \times \text{LMP}) \quad (\text{Eq. 1})$$

$$\sigma\text{MAT} = 30.6\sqrt{(1 - \text{LMP})}/r \quad (\text{Eq. 2})$$

LAA uses the correlation between leaf size (A) and mean annual precipitation (MAP), expressed as a linear relationship when both average leaf size and MAP are log-transformed (Wilf et al. 1998). Leaf areas were determined by measuring complete or near-complete leaves in photographs using ImageJ (Schneider et al. 2012). Leaves with less than 50 % of the total leaf area preserved were excluded from the analysis. MAP values were estimated using the linear regression equation (Equation 3) proposed by Wilf et al. (1998). Standard errors were calculated using regular linear regression methods. However, since the models were developed using the natural logarithm of the dependent variable, converting the results back to the original scale provides asymmetric errors (Wilf et al. 1998).

$$\ln(\text{MAP}) = 0.768 + (0.548 \times \text{MlnA}) \quad (\text{Eq. 3})$$

The CLAMP method uses canonical correspondence analysis (CCA) to statistically reconstruct past climates based on leaf morphology of modern dicot leaves, observed under known climate conditions. The physiognomic traits of a fossil leaf assemblage are scored based on the CLAMP method (see Yang et al. 2011), and palaeoclimate estimates are derived by identifying their closest analogues in CCA-defined multivariate space, calibrated with datasets of modern vegetation and climate (Wolfe 1993, Spicer 2008, Yang et al. 2011, Spicer et al. 2021). We used the Physg3brcAZ calibration dataset (Yang et al. 2011, 2015) to reconstruct key palaeoclimate variables for the Morrin Bridge fossil flora using CLAMP. These include MAT, temperature of the warmest and coldest quarters (WQT and CQT), MAP, wettest and driest month precipitation (WMP and DMP), and relative humidity (RH). Climate data were sourced from WORLDCLIM (Fick and Hijmans 2017) and integrated into the CLAMP modern calibration dataset (Yang et al. 2015). Net Primary Productivity (NPP) was reconstructed by deriving NPP values for the Physg3brcAZ calibration sites from MODIS (Running et al. 2015). Reconstructions followed standard CLAMP protocols (Wolfe 1993, Spicer

2008, Yang et al. 2011, Spicer et al. 2021) and were performed in R using CCA in the vegan package (R Core Team 2024, Oksanen et al. 2025).

Finally, the MAT and MAP results from the different physiognomic methods were combined into a single ensemble estimate. Ensemble estimates are based on resampling single-proxy results using the mean and standard deviation values (Lowe et al. 2018, West et al. 2020). In this study, resampling was done using a normal distribution for the MAT estimates, and log-transformed normal distribution for the MAP estimates. Using an ensemble of physiognomic proxies provides a more balanced palaeoclimate estimate by incorporating the strengths of multiple methods, rather than relying on any single proxy that may be subject to methodological debate.

Palaeoenvironment reconstruction

Climate data provide important context for inferring the general structure and type of forest present at a site. Whittaker (1962, 1975) proposed a widely used global biome classification system based on mean annual temperature (MAT) and mean annual precipitation (MAP). While MAT and MAP alone do not encompass the full range of variation observed in fossil leaf assemblages, Whittaker's biome model remains a useful tool for broadly categorising forest types (e.g., Flynn and Peppe 2019, West et al. 2020, Reichgelt and West 2025). The Whittaker diagram is used here to situate the reconstructed MAT–MAP values within broad ecological climate domains (e.g., temperate forest, tropical rainforest, tundra). Because these biomes are defined climatically rather than floristically, they remain appropriate for contextualizing non-analogue Cretaceous floras. Whittaker biomes were plotted for the Morrin Bridge fossil site using the *plotbiomes* R package (Ştefan and Levin 2018).

In addition, we identified the Morrin Bridge reconstructed climate to the closest modern climatic analogue. In order to do this, we applied the Closest Climatic Analogue method described by West et al. (2021, 2024). This technique generates approximately 100,000 random geodetic coordinates globally and extracts contemporary climate data – such as MAT, MAP, WQT, CQT, and DMP – from WORLDCLIM using the *dismo* package in R (Hijmans et al. 2005). As with the Whittaker plots, the Closest Climatic Analogue method cannot take other climate variables into account that result in non-analogous climatic situations, such as light regime or enhanced water-use efficiency resulting from heightened atmospheric CO₂ levels. As such, the Closest Climatic Analogue method should be interpreted as exactly that: the closest analogue in modern climate space.

Each climate variable ($x_{j,k}$) is standardised into a Z score ($Z_{j,k}$) using its global mean (μ_j) and standard deviation (σ_j), allowing differences across variables to be compared on a common scale:

$$Z_{j,k} = (x_{j,k} - \mu_j) / \sigma_j \quad (\text{Eq. 4})$$

The same standardisation is applied to the fossil site's reconstructed climate values to generate its $Z_{j,k}$ profile. For each modern location, dissimilarity to the fossil site is computed by summing the absolute differences in Z scores between that site (ZX) and the fossil site (ZF):

$$d(X, F) = \log \sum_{n=1}^4 (Z_X - Z_F)^2 \quad (\text{Eq. 5})$$

We then used Inverse Distance Weighting (IDW) in ArcGIS Pro 3.1.0 (ESRI 2023) to visualise geographic zones with climate profiles most similar to the fossil site. IDW interpolation was performed using the 12 nearest points, with a maximum search distance of 0.5°.

Systematic palaeontology

The Morrin Bridge macroflora contains a diverse assemblage of 58 taxa including a horsetail, a fern, cycadophytes (3), conifers (16), ginkgophytes (3), and angiosperms (34) (Tab. 1).

Division Monilophyta CANTINO et DONOGHUE
Family Equisetaceae MICHX. ex DC.

Genus *Equisetum* L.

***Equisetum* sp.**
Pl. 1, Fig. 1

Description. Narrow nodal rhizome, up to 132 mm long, 5–7 mm wide; round tubers, 10 mm maximum diameter.

Remarks. Horsetails are rare components of the Morrin Bridge flora and are represented by a single rhizome specimen with nodes and tubers. Similar fossils are known from the Upper Cretaceous of Alberta and were identified as *Equisetum perlaevigatum* COCKERELL (Bell 1949: pl. 6, fig. 6). *Equisetum* species are recognisable by their jointed, hollow stems and whorled leaf scars, and are typically identified based on the above ground component of the plant, primarily the leaf collars, so we refrain from identifying this fossil to species level at this time. The placement of fossil Equisetaceae into either the fossil-genus *Equisetites* STERNB. or the recent genus *Equisetum* has been much debated; Stanich et al. (2009) state that 'there are no diagnostic characters that unequivocally distinguish most species of the two genera', and Watson and Batten (1990) note that some taxa have been revised back and forth between the two genera. *Equisetites* is reserved for fossils that lack enough characters to allow a certain assignment to *Equisetum*, whereas fossils may be placed in *Equisetum* if there are enough characters to support this placement, even without anatomical evidence as with *Equisetum burchardtii* DUNKER (Watson and Batten 1990). *Equisetum* and *Equisetites* were widespread and persistent components of Late Cretaceous floras, typically inhabiting moist, lowland environments such as river margins, floodplains, and wetlands (Spicer et al. 1992, McIver and Basinger 1989, Stanich et al. 2009, Spicer and Herman 2010).

Class Polypodiopsida CRONQUIST, TAKHT. et W.ZIMM.

Unidentified fern

Pl. 1, Fig. 2

Description. Frond fragment, 19 mm long, 22 mm wide, possibly lobate pinnule, numerous veins entering basally, venation dichotomising at least twice.

Remarks. Ferns are almost entirely absent from the Morrin Bridge flora. This specimen is the sole example, represented by a frond fragment exhibiting dichotomising venation. Ferns are typically well-represented in Upper Cretaceous floras from Alberta (Bell 1949, Serbet and Rothwell 1999, 2003, 2006), suggesting that local growing conditions at Morrin Bridge may not have been favourable for their proliferation. However, their scarcity could also reflect a taphonomic bias.

**Clade Gymnosperms
Division ‘Cycadophyta’**

The term ‘Cycadophyta’ is employed here for sterile foliage of two gymnosperm orders, Cycadales and Bennettitales that are difficult to distinguish. To differentiate between the orders, cuticle analysis is needed.

Unidentified cycadophyte 1

Pl. 1, Figs 3, 4

Description. Pinnate leaf fragments, up to 58 mm long, up to 24 mm wide, narrow, closely packed parallel-sided pinnae, mostly oppositely inserted, acute apices, prominent robust rachis.

Remarks. In gross morphology these fragments resemble fossils identified by Hollick (1930) as *Pterophyllum* BRONGN. in the Upper Cretaceous deposits of Alaska.

Unidentified cycadophyte 2

Pl. 1, Fig. 5

Description. Pinnate leaf fragments, 36 mm long, 27 mm wide, pinnae curving towards apex, strong parallel venation, narrow rachis.

Remarks. This specimen differs from unidentified cycadophyte 1 in having curving pinnae, with strong parallel veins, attached to a narrow rachis but still falls within the circumscription of the gross morphological features of the *Pterophyllum* BRONGN. form genus. *Pterophyllum* was originally established for bipinnate cycad-like foliage fossils (Brongniart 1828) but is now restricted to Bennettitales leaves (Pott et al. 2007).

Family Nilssoniaceae T.KIMURA et SEKIDO

Genus *Nilssonia* BRONGN.

***Nilssonia serotina* HEER**

Pl. 1, Fig. 6

Description. Leaf fragments, 51 mm long, 30 mm wide, pinnatisect pinnules entire margined, strong parallel venation, attached to thick rachis.

Remarks. Specimens such as these were identified as *Nilssonia serotina* by Bell (1949: pl. 1, fig. 5) from Upper Cretaceous floras in Alberta. Confusion over the naming has arisen as this fossil-taxon was transferred to *Nilssoniocladus comtula* (HEER) PEPPE et HICKEY (Nilssoniaceae) (see Peppe et al. 2007), but *Nilssoniocladus* T.KIMURA et SEKIDO, was erected as a morphogenus of slender stems with shoots of attached *Nilssonia*-type leaves (Kimura and Sekido 1975). The transfer of some isolated *Nilssonia* fossil leaf species to *Nilssoniocladus* by Peppe et al. (2007) is therefore not valid as the leaves must be arranged in shoots for assignment to *Nilssoniocladus*. The fossil-genus *Nilssonia* was originally described by Brongniart (1825) based on Jurassic material from southern Sweden (Pott et al. 2007). Fossils attributable to *Nilssonia* and the leafy shoots *Nilssoniocladus* are well-known around the world in deposits ranging from the Triassic to the Cretaceous (Hollick 1930, Bell 1949, MacLeod and Hills 1991, Spicer and Herman 1996, McLoughlin 1996, Peppe et al. 2007, Pott et al. 2007, Čepičková and Kvaček 2020).

Order Ginkgoales GOROZH.

Family Ginkgoaceae ENGL.

Genus *Ginkgoites* SEWARD

***Ginkgoites pluripartitus* (SCHIMP.) SEWARD**

Pl. 1, Fig. 7

Description. Leaves, flabellate, up to 36 mm wide, up to 30 mm long. Base angle acute, base shape cuneate or decurrent; blade dissected into segments, typically 4–6 primary segments, primary segments rarely divided into secondary segments, apex of segments rounded. Venation strongly parallel, typically branched dichotomously; veins about 0.7 mm apart, 12–14 per cm.

Remarks. These fossils demonstrate similar fan-shaped outline and radiating dichotomous venation as seen in *Ginkgo adiantoides* (UNGER) HEER; however, rather than marginal notches these leaves are dissected into broad segments. Leaves of this type have been identified previously in Upper and Lower Cretaceous deposits in Western Canada as *Ginkgoites* (Bell 1949, Aulenback 2009) and *Ginkgo pluripartita* (SCHIMP.) HEER (Bell 1956: pl. 36, figs 1, 2), now synonymised to *Ginkgoites pluripartitus* (SCHIMP.) SEWARD by Watson et al. (1999).

***Ginkgoites* sp.**

Pl. 1, Fig. 8

Description. Leaves, flabellate, up to 85 mm wide, up to 53 mm long. Base angle acute, base shape cuneate or decurrent; margin entire to undulate, typically notched medially but additional notches along margin may be present, notches typically 3–4 mm deep. Venation strongly parallel, typically branched dichotomously; veins about 0.5 to 1 mm apart, 10–11 per cm.

Remarks. Leaves of this type are variously referred to as *Ginkgo dawsonii* KNOWLT. (Bell 1957), or *Ginkgo adiantoides* (Bell 1949, Tralau 1968). We follow Seward (1919) in using the form genus *Ginkgoites* for fossil ginkgoalean leaves without cuticular detail, and reserve *Ginkgo* for the extant species.

Genus *Baiera* BRAUN

Baiera sp.

Pl. 1, Fig. 9

Description. Leaves, flabellate in outline, up to 52 mm long, up to 41 mm wide; blade deeply dissected by 7–10 linear-lanceolate segments, segments up to 30 mm long, up to 4 mm wide, apex of segments rounded or bifurcated. Venation faint, parallel.

Remarks. These fossils are identified as *Baiera*, which is an extinct genus of ginkgophyte plants known from the Mesozoic, particularly the Jurassic and Cretaceous periods (Tralau 1968) and is characterised by fan-shaped leaves with deeply dissected segments and radiating dichotomous venation. The dissection between the much narrower segments is deeper in this fossil-genus than in the morphologically variable *Ginkgoites pluripartitus* (SCHIMP.) SEWARD. The revision by Watson et al. (1999) of *G. pluripartitus* demonstrates that the leaves are very variable in the depth and width of the dissections. Some are also finely dissected near the margin, but the dissection is not almost to the level of the petiole and the segments are not as thin at this level (Watson et al. 1999). A drawing of a cast of an impression fossil of a *G. pluripartitus*-like leaf from the Potomac Formation (Watson et al. 1999: fig. 4D) rather resembles *Baiera*, especially as it lacks the basal portion with the petiole. We therefore use *Baiera* here as the leaves are deeply and finely dissected almost to the level of the petiole. *Baiera* has been previously identified in both Lower and Upper Cretaceous deposits in Western Canada (Bell 1956, Koppelhus 2005). Ginkgophytes were a common and recognisable component of Late Cretaceous floras, although they were less diverse than in earlier periods.

Class Pinopsida BURNETT

Order Cupressales LINK

Family Cupressaceae GRAY

The Cupressaceae represent the majority of coniferous compression/impression fossils in the Morrin Bridge fossil flora in terms of specimen numbers. Most of these fossils are vegetative and reproductive organs of the Sequoioideae and Taxodioideae subfamilies. We consider extant as well as fossil-taxa for the morphological comparisons. One fossil-genus relevant to this study is *Parataxodium* C.A. ARNOLD et LOWTHER, which was described from the Cretaceous of Northern Alaska (Arnold and Lowther 1955). The original description is based on an assemblage of ovuliferous cones, pollen cone branches, and leafy branches (Arnold and Lowther 1955). A recent reinvestigation of the *Parataxodium wigginsii* C.A. ARNOLD et LOWTHER type and figured material has revealed that the whole-plant description of the fossil-species was based on multiple, not organically connected plant organs (Rothwell et al. 2020). These

individual organs do not come from a monotaxic plant fossil assemblage of *P. wigginsii* as previously assumed, but from a much more diverse plant bed with five distinct morphologies of Cupressaceae (Rothwell et al. 2020). At this point it is unclear which reproductive organs might belong to the vegetative shoots designated as the holotype of *P. wigginsii* (Rothwell et al. 2020). Pending a detailed reinvestigation and redescription of *P. wigginsii*, we follow Rothwell et al. (2020) and restrict the generic concept for our taxonomic comparisons to the leafy shoots only (Arnold and Lowther 1955: fig. 7, holotype).

Genus *Taxodium* RICH.

Taxodium sp.

Pl. 1, Figs 10, 11

Description. Pollen cone-bearing branchlets, arranged in panicles, branching alternate, second order branchlets subtended by falcate, folded leaf dissimilar to the subtending leaves of pollen cones, base decurrent, apex sharply acute, 4.05 mm long; pollen cones globose to obovate, 2.13–5.43 mm long (mean: 3.15 mm), 1.33–2.45 mm wide (mean: 1.83 mm), arranged helically, arising from the axils of scale-like leaves, leaves with long, decurrent bases, free part short, falcate to sigmoid-shaped, keeled, apex sharply acute, 0.996–2.55 mm long (mean: 1.60 mm).

Remarks. The fossils are characterised by globose to obovate pollen cones that are helically arranged on long, branching panicles (Pl. 1, Fig. 11), similar to those of extant *Taxodium* (Farjon 2005). Specialised pollen cone-bearing branchlets, that is fertile branchlets that exclusively bear pollen cones and their subtending leaves, can also be found in the genera *Metasequoia* HU et W.C. CHENG (Farjon 2005) and *Drumhelleria* SERBET et ROTHWELL. In contrast to *Taxodium* sp., *Metasequoia* pollen cones are arranged in a (sub-)opposite fashion (Farjon 2005). *Drumhelleria* has helically arranged pollen cones which are more elliptical than our fossils' (Serbet and Rothwell 2025). Both *Metasequoia* and *Drumhelleria* pollen cones have linear subtending leaves which are unlike the scale-like subtending leaves of *Taxodium* sp. (Pl. 1, Fig. 10). Additionally, branching of pollen cone-bearing branchlets has not been observed in *Drumhelleria* (Serbet and Rothwell 2025). Second order branching of pollen cone branchlets and scale-like subtending leaves are characteristic of the genus *Taxodium* (Schweitzer 1974), including its fossil representatives (e.g., *Taxodium wallisii* AULENB. et B.A. LEPAGE from the HCF).

Genus *Cupressinocladus* SEWARD

Cupressinocladus interruptus (NEWB.) KRASSILOV

Pl. 1, Fig. 12

Description. Flattened leafy branches and branchlets, branching opposite, leaves scale-like, decussate, facial and lateral leaves dissimilar, leaves on branches dissimilar from leaves on branchlets; basal leaves on branches monomorphic, tightly imbricate, triangular; facial leaves on branches nearly fully adpressed, narrow, barely visible, 1.89–2.24 mm long (mean: 2.05 mm), 0.32–0.70 mm wide (mean: 0.52 mm);

lateral leaves falcate to sigmoid-shaped, folded, apically free, 0.99–1.84 mm long (mean: 1.40 mm), 0.25–0.51 mm wide (mean: 0.38 mm); both with acute apices; the basal-most pair of facial leaves of branchlets is persistent after branchlet abscission, broadly triangular, apices acute to cuspidate, 0.84–1.63 mm long (mean: 1.22 mm), 0.66–1.42 mm wide (mean: 0.98 mm); lateral leaves on branchlets folded, falcate, bases obscured by preceeding facial leaves, apically free, 0.56–1.22 mm long (mean: 0.87 mm), 0.31–0.65 mm wide (mean: 0.43 mm), with acute apices.

Remarks. Morphologically similar compression/impression fossils have been described from the Lower Edmonton Formation (= HCF) as *Thuites interruptus* (NEWB.) W.A. BELL (Bell 1949) [= *Cupressinocladus interruptus* (NEWB.) KRASSILOV]. Other comparable fossils have been described as members of the fossil-genus *Mesocyparis* McIVER et BASINGER. *Mesocyparis umbonata* McIVER et AULENB. was described from three-dimensional silicifications of the HCF (McIver and Aulenback 1994). *Mesocyparis borealis* McIVER et BASINGER was recognised from the Paleocene Ravenscrag Formation, Saskatchewan, Canada (McIver and Basinger 1987), and from the Upper Cretaceous Fox Hills Formation of North Dakota (Peppe et al. 2007). A consistent opposite branching pattern distinguishes our fossils, *Mesocyparis*, and *Cupressinocladus interruptus* from extant genera of Cupressaceae *sensu stricto* (McIver and Basinger 1987). Even though the fossils have many overlapping characters with *Mesocyparis*, that fossil-genus was established based on a combination of vegetative and reproductive characters (McIver and Basinger 1987), while our fossils consist only of vegetative material. Ovuliferous cone structure is crucial for the classification of extant Cupressaceae owing to the morphological similarities of the vegetative shoots (McIver and Basinger 1987). Thus, we assign our fossils to the fossil-species *Cupressinocladus interruptus*, which was erected for leafy shoots from Spitzbergen (Schweitzer 1974).

***Cupressinocladus* sp. 1**

Pl. 1, Fig. 13

Description. Fragment of a leafy branch, leaves scale-like, dimorphic, lateral leaves falcate, folded, apices acute, facial leaves adpressed, apices acute.

Remarks. *Cupressinocladus* sp. 1 is differentiated from *Cupressinocladus* sp. 2 in a larger leaf size, more rounded lateral leaves, and the sharper divergence angle of the falcate lateral leaves. The fossil is also different from *Cupressinocladus interruptus*, a fossil-species characterised by opposite branching, leaf dimorphism between branches and branchlets, and much smaller scale-like leaves with longer decurrent bases (Schweitzer 1974). A larger, branching specimen of *Cupressinocladus* sp. 1, has not been recovered but leaf characters are unlike those of *C. interruptus*.

***Cupressinocladus* sp. 2**

Pl. 1, Fig. 14

Description. Sterile branch frond-like, branching opposite, higher order branches arising from axils of lateral leaves,

leaves scale-like, dimorphic, facial leaves adpressed, lateral leaves falcate, folded, more or less sigmoid-shaped, apically free, apices acute, bases decurrent.

Remarks. The preservation is very incomplete. This lack of morphological detail on the fossils prevents an assignment to *C. interruptus*, despite the similarities in the branching pattern and the shape and size of leaves.

Genus *Elatocladus* HALLE

***Elatocladus* sp. var. A–D**

Pl. 2, Figs 1–4

Description. Leafy branches, leaves needle-like, dorsiventrally flattened, helically to suboppositely arranged, leaf arrangement more or less distichous, bases decurrent, margins entire, apices acute to mucronate to obtuse.

Taxonomic notes: Branchlets with needle-like leaves are extremely numerous. This abundance is unsurprising given that extant needle-leaved genera such as *Glyptostrobus* ENDL., *Metasequoia*, and *Taxodium* are deciduous or semi-evergreen (Farjon 2005). Numerous fossil-taxa like *Metasequoia milleri* ROTHWELL et BASINGER, *Parataxodium wigginsii*, and *Drumhelleria kurmanniae* are argued to have been deciduous, too (Arnold and Lowther 1955, Rothwell and Basinger 1979, Basinger 1981, Serbet and Rothwell 2025). Vegetative remains of these genera are macromorphologically similar. In particular, *Taxodium* and needle-leaved branchlets of *Glyptostrobus*, *Taxus* L., and *Sequoia* ENDL. share numerous morphological characters (Ferguson 1967). These overlaps show that similar morphology may or may not correspond to phylogenetic relatedness. There is currently no reliable framework to unequivocally differentiate between leafy branches of extant taxa, let alone fossil-taxa, such as *Sequoia*, *Glyptostrobus*, *Taxodium*, *Parataxodium*, and *Drumhelleria*, in small samples. In large, preferably monotaxic, fossil assemblages, this issue can be overcome through large sample sizes which enable a better quantification of leaf characters and organic connection to reproductive material (e.g., Basinger 1981, Stockey et al. 2001). The high morphological diversity in the Morrin Bridge fossil assemblage would, thus, require micromorphological leaf characters (i.e., preserved cuticle) to provide a more reliable way to differentiate the fossil-taxa. Given that cuticles could not be recovered from coniferous fossils, we place all needle-leaved Taxodiaceae fossils within *Elatocladus*. We recognize four varieties of *Elatocladus* (A–D) based on their macromorphology; however, it is unclear at this point whether the differences are related to inter- or intraspecific variation.

***Elatocladus* sp. var. A**

Pl. 2, Fig. 1

Description. Vegetative shoots, branching alternate, branchlets with enlarged bases (if preserved), leaves needle-like, helically arranged, consistently diverging at acute angles, incompletely twisted into two ranks, apices obtuse +/- mucronate, 4.25–9.06 mm long (mean: 6.29 mm); 0.63–1.13 mm wide (mean: 0.86 mm).

Remarks. Missing mucros may be a result of the mode of preservation which could obscure such minute details as we note missing mucros also in herbarium specimens of *Metasequoia glyptostroboides* HU et W.C.CHENG (K. Halbwidl, pers. observation 2025). *Elatocladus* var. A is similar to *Drumhelleria kurmanniae* branchlets in leaf arrangement, size, and macromorphology (Serbet and Rothwell 2025). Though, as *D. kurmanniae* was described from micromorphologically and anatomically preserved specimens (Serbet and Rothwell 2025), the compression/impression fossils of *Elatocladus* var. A cannot be assigned to this fossil-species due to a lack of characters available for comparison. The fossils are also macromorphologically comparable to *Parataxodium wigginsii* in the alternate arrangement of shoots and the helical arrangement of leaves that occasionally approaches a subopposite condition (Arnold and Lowther 1955). The length of leaves overlaps between some shoot types of *Elatocladus* var. A and *P. wigginsii*, but the divergence angle of *Elatocladus* var. A is less variable (Arnold and Lowther 1955). *Elatocladus* var. A resembles Bell's (1949) *Sequoiites artus* W.A.BELL from the Upper Cretaceous Lower Edmonton Formation in the leaves' decurrent and barely constricted bases, and small size. However, *S. artus* has leaves with acute apices which display more incomplete twisting into two ranks than *Elatocladus* var. A (Bell 1949: pl 16, fig. 2).

***Elatocladus* sp. var. B**

Pl. 2, Fig. 2

Description. Vegetative shoots, leaves needle-like, narrow, helically arranged, twisted into two ranks, bases decurrent, apices obtuse, 6.39–14.63 mm long (mean: 10.32 mm), 0.79–1.21 mm wide (mean: 0.99 mm).

Remarks. *Elatocladus* var. B can be differentiated from *Elatocladus* var. A by the longer, thus, apparently more slender needle-like leaves that are oftentimes slightly recurved. They are also more consistently distichous than *Elatocladus* var. A. *Elatocladus* var. B bears superficial resemblance to Bell's (1949) *Elatocladus intermedius* (HOLLICK) W.A.BELL.

***Elatocladus* sp. var. C**

Pl. 2, Fig. 3

Description. Vegetative shoots, leaves needle-like, helically arranged, only rarely twisted into two ranks, bases decurrent, apices obtuse, 4.24–9.41 mm long (mean: 6.26 mm), 0.34–0.82 mm wide (mean: 0.66 mm).

Remarks. The leafy shoots assigned to *Elatocladus* var. C are less distichous than both *Elatocladus* var. A and *Elatocladus* var. B. The bases are not prominently twisted with the leaves diverging from the axis at less than 45°, on average. The leaves are also less densely arranged and quite narrow, resembling those of *Glyptostrobus* (following LePage 2011) or *Sequoiites artus* (Bell 1949). Alternatively, Serbet and Rothwell (2025) illustrate that juvenile branchlets of *Drumhelleria kurmanniae* display a non-distichous leaf arrangement that is different from more mature branchlets. Such a disparity between branchlets is also displayed in, for example, *Taxodium* (Farjon 2005).

***Elatocladus* sp. var. D**

Pl. 2, Fig. 4

Description. Fragment of a leafy shoot, leaves needle-like, subopposite, distichous, bases decurrent, somewhat oblique, 1.29–1.46 mm wide (mean: 1.38 mm).

Remarks. Decurrent bases that appear to be somewhat oblique and divergence angles of almost 90° distinguish *Elatocladus* var. D from *Elatocladus* var. A–C.

Unidentified Sequoioideae ovuliferous cone 1

Pl. 2, Fig. 5

Description. Ovuliferous cones, shape ellipsoidal, ovuliferous complexes helically arranged, spreading, peltate, distal ends with central depression, base pedicellate, 6.85–8.77 mm long (mean: 8.02 mm), height of distal end: 2.75–4.82 mm (mean: 3.97 mm).

Remarks. The ovuliferous complexes (OCs) are spreading, likely indicating their maturity (Pl. 2, Fig. 5). The morphological and anatomical characters of this specimen, such as the ovuliferous cones' shape, size, and persistence, indicate affinity to three genera of Sequoioideae: the fossil-genus *Drumhelleria* contemporaneous to the studied flora (Serbet and Rothwell 2025), plus modern *Sequoia* (Farjon 2005) and *Metasequoia* (Stockey et al. 2001). Even though *Metasequoia* ovulate complexes are opposite today, there is evidence of helical arrangement at least until the Paleocene (e.g., *Metasequoia foxii* STOCKEY, ROTHWELL et FALDER; Stockey et al. 2001). Associated leafy branchlets (*Elatocladus* var. A–D) have helically arranged leaves, thus, an affinity to *Drumhelleria* or *Sequoia* appears more probable. A placement in either genus is not possible at this point as the fossils lack further identifying characters and clear attachment to leafy material. However, these specimens are identified as belonging to the Sequoioideae.

Unidentified Sequoioideae ovuliferous cone 2

Pl. 2, Fig. 6

Description. Juvenile ovulate cones, ovoid, 6.36–8.32 mm long, 4.79–6.48 mm wide; one attached to a long peduncle, peduncle with short, awl-shaped leaves, closely adpressed to axis, bases decurrent, apices acute.

Remarks. These specimens are ovoid seed cones on long branchlets (Pl. 2, Fig. 6) comparable to juvenile cones of Sequoioideae. All three extant genera of Sequoioideae (*Metasequoia*, *Sequoia*, and *Sequoiadendron* J.BUCHHOLZ) have ovuliferous cones on either short branchlets (*Sequoiadendron*, *Sequoia*) or pedunculate shoots (*Metasequoia*) (Farjon 2005). Additionally, the Sequoioideae fossil-species *Drumhelleria kurmanniae* SERBET et STOCKEY from the HCF also has cones on long peduncles (Serbet and Rothwell 2025). The awl-shaped, helically arranged, nearly adpressed leaves on the branchlets of these specimens, as well as the shape of the ovuliferous cones (Pl. 2, Fig. 6), are most comparable to *Sequoia* (Farjon 2005). As Serbet

and Rothwell (2025) note the abscised linear leaves on the peduncles of mature *Drumhelleria* cones, an affinity appears unlikely due to the presence of awl-shaped leaves on the branchlets of these specimens (Pl. 2, Fig. 6). Immature seed cone material of *Drumhelleria kurmanniae* was not available for comparison. The fossils recovered at this time have incompletely preserved ovuliferous complexes. Given the importance of these structures for generic delimitation, these specimens remain unidentified, although are recognised as belonging to the Sequoioideae.

Unidentified Cupressaceae ovuliferous cone

Pl. 2, Fig. 7

Description. Mature ovuliferous cone, 12.04 mm long, 10.63 mm wide; with peduncle, 5.94 mm long, apparently four attached ovuliferous complexes.

Remarks. Four OCs per cone are common among Cupressaceae s. str. today and can be found in the genera *Austrocedrus* FLORIN et BOUTELJE, *Diselma* HOOK.F., *Libocedrus* ENDL., *Papuacedrus* H.L.LI, *Pilgerodendron* FLORIN, *Tetraclinis* MAST., *Widdringtonia* ENDL., and some individuals of *Cupressus* L., *Platycladus* SPACH, and *Juniperus* L. sect. *Sabina* SPACH (Dörken 2020). Thus, we can exclude the Taxodioideae and Sequoioideae. The fossil-genus *Mesocyparis* from the Upper Cretaceous of Canada also has four ovuliferous complexes which spread at maturity (McIver and Basinger 1987). This specimen has a distinct peduncle, differentiating it from the almost sessile ovuliferous cones of *Mesocyparis* (McIver and Basinger 1987, McIver and Aulenback 1994). Morphologically, the specimen is most similar to *Cupressus* (Dörken and Nimsch 2018), especially if the structures visible at the attachment of the peduncle at the cone were additional sterile cone scales (Pl. 2, Fig. 7). Pending retrieval of additional fossils and morphological evidence, a generic assignment is not possible at this time.

Unidentified Sequoioideae pollen cones

Pl. 2, Figs 8, 9

Description. Unbranched pollen cone-bearing branchlets with a distinctly swollen base, pollen cones elliptical, arising from axils of needle-like, linear leaves, apices of leaves frequently broken off, arrangement helical, pollen cones including basal, vegetative scale-like leaves 1.90–3.55 mm long (mean: 2.66 mm), 0.73–1.93 mm wide (mean: 1.41 mm).

Remarks. We recognise this specimen as a member of the Sequoioideae. Several morphological characters like the spiral arrangement of organs, linear needle-like leaves, and shape of the pollen cones are shared with *Drumhelleria kurmanniae* (Serbet and Rothwell 2025). However, a taxonomic comparison is challenged by the limited characters preserved in the fossils compared to the anatomically described *Drumhelleria* (Serbet and Stockey 1991, Serbet and Rothwell 2025). The fossils also share characters like the linear subtending leaves with *Juniperites gracilis* (HEER) SEWARD et V.M.CONWAY from the Upper Cretaceous Lower Edmonton Formation (Bell 1949).

From the limited number of preserved characters, it appears that this branch represents a pollen cone-bearing branch. Considering the geographic and temporal proximity to the Morrin Bridge fossil site, we suggest, as with *Drumhelleria*, an affinity with the Sequoioideae is likely a better placement than *Juniperites* BRONGN.

Family Taxaceae GRAY

Genus *Torreyites* SEWARD

Torreyites sp.

Pl. 2, Figs 10, 11

Description. Vegetative shoots, individual leaves and leaf fragments, leaves helically arranged, twisted into two ranks, linear-lanceolate, 10.42–27.40 mm long (mean: 18.92 mm), 1.81–3.26 mm wide (mean: 2.77 mm), widest in the first 1/3 of the leaf, bases decurrent, short petiole formed by twisting leaf base, apices sharply acute to cuspidate, abaxial leaf surface with two narrow, longitudinal grooves.

Remarks. The leaf characters suggest affinity with the Taxaceae or, potentially, the Cephalotaxaceae. Cuticular characters of the epidermal cells and stomatal bands are necessary for a delimitation of genera of the Taxaceae and Cephalotaxaceae (Elpe et al. 2017). The cuspidate apices, leaf size, and narrow longitudinal grooves on the abaxial leaf surfaces are most comparable to the Taxaceae (Eckenwalder 2009). As leaf cuticles are not preserved in the fossils, we refrain from placement in an extant genus and assign them to the fossil-genus *Torreyites*. These specimens do not belong to *Torreyites tyrrellii* (DAWSON) W.A.BELL described from the Upper Cretaceous of Alberta as that fossil-taxon has helically arranged, non-distichous leaves with acute apices, a prominent abaxial keel, missing deep grooves on the abaxial leaf surface, and prominent stomatal bands (Bell 1949), all dissimilar characters to the Morrin Bridge fossils.

Incertae Sedis

Genus *Conago* I.M.MILLER et HICKEY

Conago sp. 1

Pl. 2, Fig. 12

Description. Basal fragment of a coniferous ovuliferous cone, shape elongate, cone scales numerous, foliar, helically arranged, tightly imbricate, broadly triangular in shape, apices broadly acute to obtuse, some with a preserved mucro.

Remarks. The numerous, foliar cone scales and the elongated shape of the cone seen in this specimen indicate a potential affinity with the families Pinaceae or Cheirolepidiaceae, though the cone is incompletely preserved. The fossil is referred to the fossil-genus *Conago*, a fossil-genus erected for ovuliferous cones of unknown systematic affinity by Miller and Hickey (2010). However, if the fossil is not a cone but a robust branch with scale-like foliage, assignment to *Brachyphyllum* BRONGN. may be more appropriate.

***Conago* sp. 2**

Pl. 3, Fig. 1

Description. Small, ellipsoid ovulate cones, 7.83–9.77 mm long (mean: 9.06 mm), 6.22–8.55 mm wide (mean: 7.32 mm); ovuliferous complexes helically arranged, imbricate, foliar, basally narrow, spreading distally, 3.90–5.90 mm long (mean: 4.71 mm), 2.28–3.61 mm wide (mean: 2.81 mm).

Remarks. The apparently foliar ovuliferous complexes (Pl. 3, Fig. 1) are similar to *Cunninghamia* R.Br. and *Taiwania* HAYATA (Andruchow-Colombo et al. 2022). The incomplete preservation of the apices prevents a placement with either *Cunninghamia* (characteristic apiculate to cuspidate apices) or *Taiwania* (mucronate apices) (Farjon 2005). Given this incomplete preservation, the affinity of this specimen remains unknown and it is accordingly placed in the fossil-genus *Conago*.

Genus *Pagiophyllum* HEER

Three morphologies fall into the broad circumscription of the form genus *Pagiophyllum*. Fossils of this type have been variously related to the families Araucariaceae, Cheirolepidiaceae, and the Taxodiaceae (Harris 1979, also see Stockey 1982). These determinations were only possible using cuticular characters (Harris 1979). As none of the Morrin Bridge fossils have preserved cuticle, we are unable to assign *Pagiophyllum* sp. 1, *Pagiophyllum* sp. 2, and *Pagiophyllum* sp. 3 to any of the three (sub-) families.

***Pagiophyllum* sp. 1**

Pl. 3, Fig. 2

Description. Vegetative shoots, branching alternate, leaves polymorphic, morphology and divergence angle depending on branch order; all leaves helically arranged, awl-shaped to falcate with prominent abaxial keels, bases decurrent, basal leaf lamina not constricted, roughly as wide as the decurrent base, free part of leaves longer than width of decurrent base, apices acute; leaves on lower order branches with very acute angles of divergence, almost adpressed to axis, 1.79–3.66 mm long (mean: 2.69 mm), 0.62–2.8 mm wide (mean: 1.35 mm); leaves on higher order branches with less acute angles of divergence, more imbricated near the base of the branch than near the apex, 1.60–2.84 mm long (mean: 2.10 mm), 0.55–1.23 mm wide (mean: 0.76 mm).

Remarks. Leaf arrangement helical but somewhat paired distally on the shoot. The leaves are widest near the decurrent base with acute apices, which are more (basally on shoots and subtending lateral branchlets) or less (distally on shoots and first order branches) incurved (Pl. 3, Fig. 2).

***Pagiophyllum* sp. 2**

Pl. 3, Fig. 3

Description. Leafy shoots, branching alternate, leaf arrangement helical, irregularly paired, leaves falcate to awl-shaped, base of free lamina roughly as broad as the decurrent base, tapering towards apex, apices acute, more or

less incurved, free part of the leaf longer than the decurrent base is wide, 1.74–3.41 mm long (mean: 2.33 mm), 0.56–1.52 mm wide (mean: 0.87 mm).

Remarks. The leafy shoots of *Pagiophyllum* sp. 2 are similar to *Pagiophyllum* sp. 1 in their helical but somewhat irregularly paired leaf arrangement and in the falcate to awl-shaped leaves with wide, decurrent bases, and acute, more or less incurved apices (Pl. 3, Fig. 3). Branches of *Pagiophyllum* sp. 2 have a more fragile appearance than *Pagiophyllum* sp. 1 due to the larger spaces between the leaves and the smaller vertical thickness of the leaves in comparison to their lengths, which both lead to less imbrication. Distally on branches, leaves appear to be somewhat distichous.

***Pagiophyllum* sp. 3**

Pl. 3, Fig. 4

Description. Leafy shoots, branching alternate, leaves helically arranged, more or less distichous, imbrication minimal, restricted to base of the branch, leaves longest near the base of the branch, getting shorter towards the apex; leaves falcate to awl-shaped, base decurrent, leaf lamina not constricted above decurrent base, free part of leaf markedly longer than width of the base, leaves with prominent abaxial keel, apices acute, slightly incurved, 2.18–5.83 mm long (mean: 3.70 mm), 0.95–2.00 mm wide (mean: 1.35 mm).

Remarks. *Pagiophyllum* sp. 3 is similar to *Pagiophyllum* sp. 1 in the robustness and shape of the leaves, but it is also resembles *Pagiophyllum* sp. 2 in the more or less distichous arrangement of leaves on the branch. In contrast to *Pagiophyllum* sp. 2, the leaves are longest and spread the widest near the base of the shoot and then become smaller and less spreading towards the apex in *Pagiophyllum* sp. 3 (Pl. 3, Fig. 4). Such a pattern is not observable in *Pagiophyllum* sp. 2. An additional difference is the overall larger size of the leaves in *Pagiophyllum* sp. 3.

Comparison. Bell (1949) described *Cryptomerites lambii* W.A.BELL from leafy shoots with attached ovuliferous cones from Paleocene sediments of the Paskapoo Formation and from Paleocene strata overlying the Upper Cretaceous Brazeau Formation, both in Alberta. While no ovuliferous complexes were found attached to leafy shoots of *Pagiophyllum* sp. 1–3, several similarities in the morphology and arrangement of the leaves are noted: leaves with helical arrangement, often falcate or awl-shaped, ascending to spreading, with decurrent bases (Bell 1949). However, there is no leaf micromorphological description (*Cryptomerites lambii*) and no cuticle available (*Pagiophyllum* sp. 1–3) for more extensive comparison between the fossil-taxa. Notably, *Cryptomerites* BRONGN. is in need of revision after a complicated history that now places it within the Permian conifer genus *Ullmannia* GOEPP. (Doweld 2016, Herendeen 2017). The lack of reproductive material and micromorphological information on *Pagiophyllum* sp. 1–3 are confounding factors in the identification. Many conifers have polymorphic branches and leaves, and the particular morphologies of *Pagiophyllum* sp. 1–3 are common to a variety of genera – for example,

Glyptostrobus, *Taiwania*, and *Athrotaxis* D.DON (Farjon 2005). Extant *Taiwania* displays shoots of the *Pagiophyllum* sp. 1 and *Pagiophyllum* sp. 3 types as well as a broader version of the *Pagiophyllum* sp. 2 type.

Unidentified vegetative shoot

Pl. 3, Fig. 5

Description. Basal fragment of vegetative shoot, basal leaf pair subulate and narrow; other leaves helically arranged, tightly imbricated, falcate, widest near the base, tapering towards the apex, bases decurrent, apices acute, 1.72–2.33 mm long (mean: 2.07 mm).

Remarks. The tightly imbricated triangular leaves resemble the basal leaves of *Pagiophyllum* sp. 1 branches; however, *Pagiophyllum* sp. 1 specimens do not exhibit a basal leaf pair with subulate leaves, as seen in this specimen. The limited morphological characters do not allow a taxonomic placement for this fossil at this time.

Clade Angiosperms

Clade Monocots

Incertae sedis

Genus *Monocotylophyllum* E.REID et M.CHANDLER

Monocotylophyllum sp. 1

Pl. 3, Fig. 6

Description. Leaves fragmentary, up to 54 mm long, up to 12 mm wide, microphyllous. Margin untoothed. Primary venation parallel, numerous, spaced 0.35–0.65 mm apart. Secondary veins form distantly spaced sets of transverse veins that cross between sets of parallel veins; secondary veins typically offset, secondary vein course straight to convex.

Remarks. These fossils consist of linear fragments of larger leaves with strong, dense, parallel venation (Pl. 3, Fig. 6). Fragments of this type are previously known from the Upper Cretaceous deposits of Alberta and were identified as *Typha* L. (Bell 1949: pl. 12, fig. 8), a typical assignment for remains of this type, based primarily on the venation. However, this identification requires further scrutiny pending the discovery of better-preserved material. Bell's (1949) material, as well as ours, lacks diagnostic traits. As such we refrain from any formal assignment to *Typha* at this time, and instead assign the fossils to the fossil-genus *Monocotylophyllum* E.REID et M.CHANDLER.

Monocotylophyllum sp. 2

Pl. 3, Fig. 7

Description. Leaf fragmentary, up to 71 mm long, up to 39 wide. Margin appears untoothed but poorly preserved. Primary venation parallel, numerous, space 0.65 mm apart. Secondary veins form numerous sets of transverse veins that cross between the primary veins forming small boxes; secondary veins even to offset, secondary vein course straight.

Remarks. These specimens are represented by fragmentary remains of much larger leaves (Pl. 3, Fig. 7). These differ from *Monocotylophyllum* sp. 1 in that the leaves appear to be two to three times as wide and have much finer parallel venation. Fragments of this kind, known from Upper Cretaceous and Paleocene sediments in North America, are sometimes identified as belonging to the Araceae (Bogner et al. 2007). Inflorescence material belonging to the aroids has been previously described from the Horseshoe Canyon Formation (Bogner et al. 2005). However, we refrain from any such assignment at this time pending the discovery of more diagnostic fossils and instead assign them to *Monocotylophyllum*.

Grade Dicots

Family Platanaceae T.LESTIB.

Genus *Platanites* E.FORBES ex W.H.BAILY

Platanites cf. *P. marginatus* (LESQ.) K.R.JOHNSON

Pl. 3 Figs 8, 9

Description. Leaves fragmentary, petiolate, blade attachment marginal, preserved length about 50–63 mm, preserved width about 60–64 mm, size notophyll, shape appears ovate, base symmetrical; margin toothed, serrate; base angle obtuse, base shape cuneate. Primary venation appears palinactinodromous, three basal veins; simple agrophic veins present. Major secondary venation craspedodromous, interior secondaries absent; major secondary vein spacing gradually increasing proximally, variation of major secondary vein angle to midvein uniform; major secondary vein attachment to midvein decurrent. Tertiary venation mixed percurrent; tertiary vein course convex; tertiary vein angle variability consistent. Tooth spacing regular, one order of teeth, 4 teeth per centimeter; sinus shape rounded; tooth shape concave-convex.

Remarks. These leaves are easily recognised by their distinctive decurrent base, basal venation, the narrow angle of the basal veins, and the characteristic chevron shaped pattern of tertiary venation. *Platanites marginatus* (LESQ.) K.R.JOHNSON [= *Cissus marginata* (LESQ.) R.W.BR.] is a common component of many Upper Cretaceous floras from western North America (e.g., as *Viburnum marginatum* KNOWLTON in Lesquereux 1873, as *Acer collieri* HOLLICK in Hollick 1930, as *Platanus? newberryana* HEER in Capellini and Heer 1866, and as *Platanus affinis* (LESQ.) LESQ. (Bell 1957, Johnson 1996, 2002)). The leaves of *Platanites marginatus* and *Platanites reynoldsii* (NEWB.) MANCHESTER are difficult to differentiate, especially when they are poorly preserved (Brown 1962, Manchester 2014). However, *P. marginatus* leaves have a narrower angle between the primary and secondary veins than is typical of *P. reynoldsii*, a feature present in our specimens of *Platanites* (Pl. 3, Fig. 9). As the available material is incomplete, we suggest comparison with *Platanites marginatus* at this time and refer the specimens to *Platanites* cf. *P. marginatus*. Leaves referable to the Platanaceae are common, and often distinctive, angiosperm fossils found in Upper Cretaceous deposits of North America (Bell 1949, Manchester 1986, Graham 1993, Maslova et al. 2005, Huegele and Wang 2023).

Genus *Pseudoprotophyllum* HOLLICK

Pseudoprotophyllum sp.

Pl. 4, Figs 1, 2

Description. Leaves fragmentary, petiolate, blade attachment marginal or semi-peltate, preserved length about 80 mm, preserved width about 78 mm, size mesophyll; margin appears toothed or weakly crenate; base angle obtuse, base shape concave and decurrent. Primary venation palinactinodromous, with three basal veins. Major secondary venation appears craspedodromous, interior secondaries absent, major secondary vein spacing increasing proximally, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary venation mixed percurrent, tertiary vein course convex to sinuous.

Remarks. These leaves do not have the distinctive decurrent base and tightly angled basal venation observable in specimens identified as *Platanites* cf. *P. marginatus*. Neither do these leaves have the distinctive decurrent bases typical of the terminal leaflets of *Platanites reynoldsii* (Manchester 2014: fig. 6). Rather, these leaves are most similar to the fossil-genus *Pseudoprotophyllum* HOLLICK, a member of the Platanaceae known from the higher latitudes in east Asia and North America. The fossil-genus *Pseudoprotophyllum* was established by Hollick (1930) based on fossil leaf material recovered from Cenomanian–Turonian strata on the Alaska Peninsula. It is distinguished by leaves exhibiting distinctive basal veins, dentate margins, craspedodromous venation, and typically peltate leaf bases, although apeltate forms do also occur (Golovneva 2009). The type species, *Pseudoprotophyllum boreale* (DAWSON) HOLLICK, originally named *Protophyllum boreale* DAWSON, was first described from the Upper Cretaceous Dunvegan Formation in Western Canada (Dawson 1883, Golovneva 2009). Our specimens are only partially preserved and are missing the apical portion of the leaves; however, the specimens have characteristic basal venation and bases that appear nearly peltate or semi-peltate and are similar to *Pseudoprotophyllum* leaves figured by Golovneva (2009) from the Upper Cretaceous of northern Asia.

Genus *Platanophyllum* FONTAINE

Platanophyllum sp.

Pl. 4, Fig. 3

Description. Leaves, petiolate, blade attachment marginal, preserved length about 73–80 mm, width 36–40 mm, size notophyll, L : W ratio 2 : 1, shape elliptic, medially symmetrical, basally symmetrical; margin toothed, serrate; base angle acute, base shape concave. Primary venation pinnate, with one basal vein, compound agrophic veins present. Major secondary venation craspedodromous, minor secondary venation craspedodromous, major secondary vein spacing gradually increasing proximally, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent; tertiary venation mixed percurrent. Tertiary vein angle variability consistent. Tooth spacing regular, one order of teeth, 3 to 4 teeth per centimeter, sinus shape rounded, tooth shape concave-convex.

Remarks. These leaves are assigned to the form genus *Platanophyllum* FONTAINE. Fontaine (1889) established the fossil-genus *Platanophyllum* to encompass leaves that are broadly similar to Platanaceae in form but cannot be confidently assigned to the genus *Platanus*. They are characterised by an ovate to elliptic lamina, a cuneate to convex base, pinnate primary venation, well-developed craspedodromous secondary venation that branches at regular intervals, and a toothed margin composed of serrate to crenate teeth with rounded sinuses (Pl. 4, Fig. 3). Similarly described leaves assigned to the form genus were identified by Arens and Allen (2014) from the Hell Creek Formation. However, unlike their morphotype, our specimens exhibit well-developed agrophic veins – a feature commonly found in both crown-group members and most fossil representatives of the genus (Arens and Allen 2014). Bell (1949) identified a single leaf to the fossil-genus *Platanophyllum* and determined that it was too fragmentary to figure; however, he did provide a brief description of a leaf with characters that are not present in our specimen (i.e., a deeply dissected trilobed leaf).

Genus *Platananthus* MANCHESTER

cf. *Platananthus* sp.

Pl. 4, Fig. 4

Description. Inflorescence (?), spherical to subspherical, approximately 8 mm in diameter, consisting of a spherical disc or central receptacle surrounded by possible florets.

Remarks. This fossil is a compact structure that appears to be composed of numerous small, densely packed florets, attached to a central receptacle (Pl. 4, Fig. 4). The overall organisation and form is consistent with specimens regarded as Platanaceae infructescences, such as *Platananthus* MANCHESTER, and such fossils are well-known from Cretaceous and Paleogene deposits in North America (Bell 1949, Manchester 1986).

Family Betulaceae GRAY

Genus *Corylites* J.S.GARDNER ex SEWARD et HOLTUM

Corylites sp.

Pl. 4, Fig. 6

Description. Leaf fragmentary, apex angle acute, apex shape appears acuminate; margin toothed, serrate. Primary venation pinnate (?). Major secondary venation craspedodromous, major secondary vein spacing increasing proximally, major secondary vein attachment to midvein excurrent. Tertiary venation mixed percurrent, tertiary vein course convex. Tooth spacing regular, two orders of teeth, 2 to 3 teeth per centimeter, sinus shape rounded, tooth shape concave-convex or concave-retroflexed.

Remarks. Although represented by only a partial specimen, it closely resembles fossil leaves identified as *Corylus* L. from the Hell Creek Formation (Johnson 2002). However, due to the fragmentary nature of the material and the difficulty of confidently assigning isolated leaves to extant genera, we

refrain from using the modern genus *Corylus*. Instead, we assign these specimens to the form genus *Corylites* J.S.GARDNER ex SEWARD et HOLTUM. Gardner (1887) introduced the generic name *Corylites* for fossil leaves from the early Paleocene flora of the Isle of Mull that bear a strong resemblance to those of modern *Corylus*, establishing the genus to accommodate leaves of this morphology in cases where their precise systematic placement could not be determined (Boulter and Kvaček 1989, Moiseeva 2008). However, leaves of this type are generally accepted as belonging to the Betulaceae based on their similarity to modern *Corylus*, a practice we follow here (Crane 1981, Manchester and Shuang-Xing 1996, Manchester and Chen 1998, Manchester et al. 2004). The Morrin Bridge specimen shares characteristics with the diagnosis for *Corylites*, including the craspedodromous venation with straight veins that terminate in principle teeth, a compound serrate margin, and an acuminate leaf apex (Boulter and Kvaček 1989, Moiseeva 2008). Leaves attributed to the Betulaceae are known from Upper Cretaceous deposits in British Columbia, Canada, the western Dakotas in the USA, and northeastern Russia (Bell 1957, Johnson 2002, Moiseeva 2008).

Family Cercidiphyllaceae ENGL.

Genus *Jenkinsella* E.REID et M.CHANDLER

Jenkinsella arctica (HEER) W.A.BELL

Pl. 4, Fig. 5

Description. Fruit, ellipsoidal, about 11 mm long, about 5.3 mm wide; apex acute; base rounded.

Remarks. This specimen resembles material previously identified as *Jenkinsella arctica* (HEER) W.A.BELL from Late Cretaceous deposits in Alberta (Bell 1949). *Jenkinsella arctica* is a fossil-species of follicular fruits from the Upper Cretaceous and Paleocene of the Northern Hemisphere (Golovneva and Alekseev 2017). Bell (1949) proposed to unite fruits associated with *Trochodendroides* leaves under the name *Jenkinsella arctica*, although this binomial was not adopted by others until recently (see Golovneva and Alekseev 2017). *Jenkinsella arctica* encompasses dispersed follicular fruits and racemose infructescences typically associated with *Trochodendroides* leaves. The fruits are ellipsoidal to obovate, typically bearing subparallel longitudinal ridges and fine transverse striations, and are often preserved in spirally arranged racemes. Although these fruits show variability in size and shape across different localities, such differences are insufficient for separating them into distinct species, making *J. arctica* a broadly defined morphospecies for these *Cercidiphyllum*-like fossils.

Genus *Trochodendroides* E.W.BERRY

Trochodendroides arctica (HEER) E.W.BERRY

Pl. 4, Figs 7–9

Description. Leaves, petiolate, blade attachment marginal, length 27 to 41 mm, width 33 to 56 mm, size microphyll to

notophyll, L : W ratio 0.6 : 1 to 1 : 1, shape ovate or orbiculate, medially symmetrical, basally symmetrical; margin toothed, serrately crenate; apex angle obtuse, apex shape rounded, base angle obtuse, base shape straight or concave. Primary venation basal actinodromous, with five basal veins. Major secondary veins semicraspedodromous, major secondary vein spacing irregular, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary venation reticulate. Tooth spacing regular, one order of teeth, 2 to 3 teeth per cm, sinus shape rounded, tooth shape convex-convex or retroflexed-convex.

Remarks. Fossil leaves assigned to *Trochodendroides arctica* (HEER) E.W.BERRY are common elements in floras from the Upper Cretaceous and lower Paleogene in North America and eastern Asia (Berry 1935, Bell 1949, Johnson 2002, West et al. 2019, Zolina and Golovneva 2023). Leaves of *Trochodendroides arctica* are typically broad, ovate or reniform, with crenate or rarely serrate margins, and semicraspedodromous venation, a combination of characters that aligns with our specimens (Pl. 4, Figs 7–9). While originally named for its superficial resemblance to leaves of the Trochodendraceae, leaves assigned to *Trochodendroides* BERRY are more commonly attributed to the Cercidiphyllaceae, based on morphological similarities with modern *Cercidiphyllum* SIEBOLD et ZUCC. However, this assignment remains uncertain due to the lack of associated reproductive structures. Although, leaves previously described as *Trochodendroides*, as well as leaves assigned to the modern genus *Cercidiphyllum*, are known from the Paleocene of Alberta (now *Joffrea speirsii* P.R.CRANE et STOCKEY), and have been found with attached reproductive elements that belong to the Cercidiphyllaceae (Crane and Stockey 1985). Thus, although no reproductive structures are preserved in the Morrin Bridge material, assigning these leaves to the Cercidiphyllaceae remains a reasonable interpretation given their close morphological correspondence to previously described material and the well-documented Paleocene occurrences (Manchester 2014, Zolina and Golovneva 2023). Bell (1949) previously identified *Trochodendroides arctica* from the Upper Cretaceous Lower Edmonton Formation (now the Edmonton Group, including the HCF) in Alberta. Species of *Trochodendroides* are well known from other Upper Cretaceous deposits in North America (Lesquereux 1878, Ward 1886, Newberry 1898, Berry 1930, Brown 1939, Bell 1957, 1963, 1965, Johnson 2002).

Genus *Archeampelos* McIVER et BASINGER

cf. *Archeampelos* sp.

Pl. 5, Figs 1, 4

Description. Leaf, leaf attachment petiolate, blade attachment marginal, length about 65 mm, preserved width about 58 mm, size notophyll, laminar L:W ratio about 1 : 1, shape orbiculate; margin toothed, serrately crenate; apex angle obtuse, apex shape straight, base angle obtuse, base shape concave. Primary venation basal actinodromous, with three (?) basal veins, compound archophic veins present. Major secondary

veins craspedodromous, major secondary vein spacing regular, variation of major secondary veins to midvein uniform, major secondary vein attachment to midvein excurrent. Tooth spacing regular, two orders of teeth, 1 tooth per cm, sinus rounded, tooth shape convex-convex.

Remarks. This leaf shares many features with the fossil-genus *Archeampelos* McIVER et BASINGER, a fossil-taxon common in lower Paleocene floras from North America (McIver and Basinger 1993, Manchester 2014). Given the morphological similarities between our specimen (Pl. 5, Figs 1, 4) and the fossil-genus *Archeampelos*, we refer it to cf. *Archeampelos*. Originally considered part of the Vitaceae, *Archeampelos* was later reassigned to the Cercidiphyllaceae based on foliar characteristics (Manchester 2014).

Family Trochodendraceae EICHLER

Genus *Zizyphoides* SEWARD, V.M.CONWAY ex T.JOHNSON

Zizyphoides flabella (NEWB.) P.R.CRANE,
MANCHESTER et DILCHER
Pl. 5, Fig. 2

Description. Leaf, leaf attachment petiolate, blade attachment marginal, length 48 mm, width 37 mm, size microphyll, L : W ratio about 1.3 : 1, shape elliptic, medially symmetrical, basally symmetrical; margin toothed, serrately crenate; apex angle obtuse, apex shape straight, base angle acute, base shape concavo-convex. Primary venation basal actinodromous, with five basal veins. Major secondary veins festooned semicraspedodromous, major secondary vein spacing regular, variation of major secondary angle to midvein uniform, major secondary attachment to midvein excurrent. Tertiary venation not observable. Tooth spacing regular, one order of teeth, 3 teeth per cm, sinus angular, tooth shape convex-convex.

Remarks. The fossil-genus *Zizyphoides* SEWARD et V.M.CONWAY ex T.JOHNSON, is common in Upper Cretaceous and lower Paleogene deposits in North America (Crane et al. 1991, Zolina et al. 2021). *Zizyphoides* is a genus of fossil leaves typically characterised by elliptical to orbicular laminae with actinodromous venation and entire to irregularly crenate or dentate margins. This description aligns well with the specimens from Morrin Bridge (Pl. 5, Fig. 2). The fossil-genus was initially confused with modern taxa such as *Ziziphus* MILL.; the revised concept, especially following the association of *Zizyphoides*-type leaves with *Nordenskiöldia* HEER fruits, clarified its placement within the Trochodendraceae (Crane et al. 1991). Leaves of this type have been previously identified from Upper Cretaceous deposits in Alberta as *Zizyphoides colombii* (HEER) SEWARD et V.M.CONWAY by Bell (1949), from what he termed the 'post-Brazeau Beds', which included deposits belonging to both the Upper Cretaceous Edmonton Formation (now Edmonton Group) and the Paleogene Paskapoo Formation. *Zizyphoides colombii* was later synonymised by Crane et al. (1991) with *Zizyphoides flabella*, a cosmopolitan fossil-species known from both Upper Cretaceous and Paleogene deposits from North America (Crane et al. 1991 and references therein, Johnson 2002).

Incertae Sedis

Genus *Dicotylophyllum* SAPORTA ex WARD

Dicotylophyllum sp. 1
Pl. 5, Fig. 3

Description. Leaves fragmentary; margin toothed, serrately crenate; apex angle acute, apex shape straight, base not preserved. Primary venation pinnate (?). Major secondary venation craspedodromous, major secondary vein spacing regular, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary venation opposite percurrent, tertiary vein course straight. Tooth spacing regular, one order of teeth, 2 teeth per cm, sinus shape rounded, tooth shape convex-straight.

Remarks. *Dicotylophyllum* sp. 1 bears relatively large, prominent crenate teeth with J-shaped sinuses, each enervated by a single unbranching secondary vein (Pl. 5, Fig. 3). The fragmentary nature of the material, preserving only the apical portion of the leaves, limits taxonomic resolution and precludes any formal assignment.

Dicotylophyllum sp. 2
Pl. 5, Fig. 5

Description. Leaf, blade attachment marginal, length 142 mm, width 99 mm, size mesophyll, L : W ratio about 1.5 : 1, shape ovate; margin toothed, serrate; apex angle acute, apex shape straight, base angle obtuse, base shape appears rounded. Primary venation pinnate, with one basal vein, simple agrophic veins present. Major secondary venation craspedodromous, major secondary vein spacing irregular, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tooth spacing regular, one order of teeth, 2 teeth per cm, sinus rounded, tooth shape concave-convex or straight convex.

Remarks. *Dicotylophyllum* sp. 2 is characterised by its large size, serrated, margin craspedodromous venation, and a convex base (Pl. 5, Fig. 5). Some of the teeth appear to have darkened apices suggesting the teeth were glandular.

Dicotylophyllum sp. 3
Pl. 5, Figs 6–7

Description. Leaves, petiolate, blade attachment marginal, length 51 to 98 mm, width 29 to 63 mm, size microphyll to mesophyll, L : W ratio about 1.5 : 1 to 1.7 : 1, shape obovate to ovate, medially symmetric, basally symmetric or rarely asymmetric, unlobed; margin toothed in the distal portion of the lamina, serrately crenate; apex angle obtuse, apex shape rounded, base angle obtuse or rarely acute, base shape convex or rounded. Primary venation suprabasal actinodromous, with three basal vein, compound agrophic veins present. Major secondary veins craspedodromous, major secondary vein spacing irregular, variation of major secondary angle to

midvein uniform, major secondary attachment to midvein decurrent. Tertiary veins alternate percurrent. Tooth spacing regular, one order of teeth, 1 to 3 teeth per cm, sinus rounded, tooth shape convex-convex.

Remarks. *Dicotylophyllum* sp. 3 is characterised by an ovate to obovate leaf shape, suprabasal actinodromous venation, and prominent crenate teeth restricted to the upper third of the lamina (Pl. 5, Figs 6, 7). In overall shape and venation, it resembles leaves referred to *Platanophyllum* and *Dicotylophyllum* sp. 12, but it is readily distinguished by the presence, size, and shape of the teeth in the apical region of the lamina.

***Dicotylophyllum* sp. 4**

Pl. 5, Fig. 8

Description. Leaf fragmentary, preserved length about 52 mm, preserved width about 41 mm, preserved size notophyll; base angle probably obtuse, base shape appears rounded; margin toothed in the distal portion of the leaf, crenate or undulate. Primary venation appears pinnate, with one basal vein, and simple agrophic veins present. Major secondary veins probably craspedodromous, major secondary vein spacing regular, variation of major secondary vein angle to midvein uniform; major secondary vein attachment to midvein decurrent. Tertiary veins poorly preserved but appear opposite percurrent. Tooth spacing regular, one order of teeth, 2 teeth per cm, sinus rounded, tooth shape convex-convex.

Remarks. *Dicotylophyllum* sp. 4 is represented by a partial leaf that is untoothed in the lower half of the leaf and has small crenate teeth in the upper half of the leaf (Pl. 5, Fig. 8). The agrophic veins are not as strong as those found in *Dicotylophyllum* sp. 9, and the strongly diverging basal veins are also absent.

***Dicotylophyllum* sp. 5**

Pl. 6, Fig. 1

Description. Leaf, leaf attachment petiolate, blade attachment marginal, length 100 to 109 mm, width 60 to 70 mm, size mesophyll, L : W ratio 1.7 : 1, shape ovate, medially symmetric, base asymmetric; unlobed, margin toothed, serrate; apex angle acute, apex shape straight, base angle obtuse, base shape appears concave. Primary venation pinnate, with one basal vein, simple agrophic vein present. Major secondary veins craspedodromous, major secondary vein spacing irregular, variation of major secondary angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary veins alternate percurrent. Tooth spacing regular, one order of teeth, 4 teeth per cm, sinus shape rounded, tooth shape concave-convex.

Remarks. *Dicotylophyllum* sp. 5 is characterised by pinnate primary venation, craspedodromous secondary venation, craspedodromous agrophic veins, a serrated margin, ovate leaf shape, and straight apex shape (Pl. 6, Fig. 1). This suite of morphological characters readily differentiates *Dicotylophyllum* sp. 5 from other leaf taxa occurring in the assemblage.

***Dicotylophyllum* sp. 6**

Pl. 6, Fig. 2

Description. Leaf fragmentary, preserved length about 98 mm, preserved width about 55 mm, size mesophyll, L : W ratio about 1.75 : 1, shape elliptic, medially symmetric, base asymmetric, unlobed; margin toothed, serrate; apex angle acute, apex shape straight or weakly rounded, base angle obtuse. Primary venation pinnate, with 1 basal vein, simple agrophic veins present. Major secondary veins craspedodromous, major secondary vein spacing regular, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tooth spacing regular, one order of teeth, 3 teeth per cm, sinus shape rounded, tooth shape concave-convex or convex-convex.

Remarks. *Dicotylophyllum* sp. 6 is characterised by a serrated margin, elliptic shape, and acute apex (Pl. 6, Fig. 2). Leaves assigned to *Dicotylophyllum* sp. 6 share some features with leaves referred to *Platanophyllum*, but are overall broader and have much larger teeth and wider sinuses. This leaf also shares some similarity with *Dicotylophyllum* sp. 5, but differs in shape, as *D.* sp. 5 is strongly ovate, whereas *D.* sp. 6 is elliptic, and is overall narrower. Further, *Dicotylophyllum* sp. 6 has fewer teeth per cm than does *D.* sp. 5 in the basal portion of the leaf, a shorter somewhat weakly rounded apex, and more regular/numerous secondary veins.

***Dicotylophyllum* sp. 7**

Pl. 6, Figs 3, 7

Description. Leaf fragmentary, petiolate, blade attachment marginal, preserved length about 37 to 67 mm, preserved width about 30 to 54 mm, size microphyll to notophyll, L : W ratio about 1.2 : 1, shape ovate, appears medially symmetric, base symmetrical; margin toothed, serrately crenate; apex angle obtuse, apex shape not preserved, base angle obtuse, base rounded or decurrent. Primary venation basal actinodromous, with three basal veins, compound agrophic veins present. Major secondary veins craspedodromous, major secondary vein spacing regular, variation of major secondary angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary veins opposite percurrent, with a straight vein course. Tooth spacing regular, with one order of teeth, 4 to 6 teeth per cm, sinus shape rounded, tooth shape convex-convex, teeth appear glandular.

Remarks. *Dicotylophyllum* sp. 7 is characterised by serrated teeth along the margin in the upper 1/2 to 1/3 of the lamina, an ovate to wide ovate leaf shape, a rounded to decurrent base, and basal actinodromous primary venation (Pl. 6, Figs 3, 7). In one instance, a leaf assigned to *Dicotylophyllum* sp. 7 appears to have incipient lobes (Pl. 6, Fig. 3), but this character may be the result of leaf damage. The same leaf also shows glandular teeth in the upper portion (Pl. 6, Fig. 3). Other leaves assigned to this fossil-taxon are not as well preserved, and the presence of glandular teeth in these specimens is not known.

***Dicotylophyllum* sp. 8**

Pl. 6, Fig. 4

Description. Leaf fragmentary, preserved length about 134 mm, preserved width about 106 mm, size mesophyll, L : W ratio about 1.2 : 1, shape appears ovate; margin toothed in the distal portion of the lamina, crenate; base angle obtuse, base shape rounded or weakly cordate. Primary venation pinnate, with one basal veins, simple agrophic veins present. Major secondary venation craspedodromous, major secondary vein spacing irregular, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary veins opposite percurrent, with a convex course or forming chevrons. Tooth shape convex-convex.

Remarks. *Dicotylophyllum* sp. 8 is a large, pinnate leaf with two teeth visible near the apex and an untoothed basal portion; the remainder of the margin is not preserved (Pl. 6, Fig. 4). Although it shares some overall similarity with leaves assigned to *Dicotylophyllum* sp. 9, it differs in the agrophic venation, with the basal agrophic veins showing a tendency to branch rather than forming the strongly looping pattern observed in *Dicotylophyllum* sp. 9.

***Dicotylophyllum* sp. 9**

Pl. 6, Fig. 5

Description. Leaf, petiolate, blade attachment marginal, length 40 to 68 mm, width 27 to 60 mm, size microphyll to notophyll, L : W ratio 1 : 1 to 1.5 : 1, shape elliptic to ovate, medially symmetric, base symmetrical or asymmetrical; margin untoothed; apex angle obtuse, apex shape rounded, base angle obtuse, base shape rounded or convex. Primary venation pinnate, with one basal vein, simple agrophic veins present. Major secondary veins brochidodromous, major secondary vein spacing regular, variation of major secondary angle to midvein uniform, major secondary vein attachment to midvein decurrent. Tertiary veins appear alternate percurrent, with a convex course.

Remarks. *Dicotylophyllum* sp. 9 is a common dicot leaf found at the Morrin Bridge fossil locality. It is characterised by an untoothed margin, elliptic to ovate leaf shape, a rounded to convex base, strong looping agrophic veins in the basal portion of the leaf, and the basal most secondary veins always begin at the point of petiole insertion (Pl. 6, Fig. 5).

***Dicotylophyllum* sp. 10**

Pl. 6, Fig. 6

Description. Leaf fragmentary, petiolate, blade attachment marginal, length 60 mm, preserved width about 54 mm, size notophyll, L : W ratio about 1.1 : 1, shape obovate; margin untoothed; apex angle obtuse, apex shape rounded, base angle obtuse. Primary venation pinnate, with one basal vein. Poorly preserved major secondary veins brochidodromous.

Remarks. *Dicotylophyllum* sp. 10 is characterised by an untoothed margin, obovate shape, and a rounded apex. The specimen is fragmented, and the base of the leaf is not well-preserved, which precludes any precise identification.

***Dicotylophyllum* sp. 11**

Pl. 6, Fig. 8

Description. Leaf fragmentary, preserved length about 55 mm, preserved width about 31 mm, size microphyll, L : W ratio about 1.75 : 1, shape elliptic; margin untoothed. Primary venation appears pinnate. Major secondary veins brochidodromous, major secondary vein spacing irregular, variation of major secondary vein angle to midvein uniform, major secondary attachment to midvein excurrent. Tertiary veins appear opposite percurrent.

Remarks. *Dicotylophyllum* sp. 11 is characterised by an untoothed margin and brochidodromous venation. Similar leaves attributed to the Rhamnaceae were figured by Bell (1949), however, those leaves were from Paleocene deposits. Precise identification is precluded by the fragmentary preservation of the material.

***Dicotylophyllum* sp. 12**

Pl. 6, Fig. 9

Description. Leaf fragmentary, petiolate, blade attachment marginal, length 54 to 77 mm, preserved width about 36 to 51 mm, size microphyll to notophyll, L : W ratio about 1.5 : 1, shape elliptic to obovate, base symmetrical; margin untoothed; apex angle obtuse, apex shape rounded, base angle obtuse, base shape concave, cuneate, or rounded. Primary venation pinnate, with one basal vein, simple agrophic veins present. Major secondary veins brochidodromous, major secondary vein gradually increasing proximally, variation of major secondary vein angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary veins opposite percurrent, with a straight to convex vein course.

Remarks. *Dicotylophyllum* sp. 12 is characterised by an untoothed margin, elliptic to obovate leaf shape, and that the basal most secondary veins always begin above the point of petiole insertion. *Dicotylophyllum* sp. 12 shares some similarities with leaves referred to *Platanophyllum* and *Dicotylophyllum* sp. 3, such as leaf shape and venation, but lacks the large apical teeth found in *Dicotylophyllum* sp. 3, and the serrated margin of *Platanophyllum*.

***Dicotylophyllum* sp. 13**

Pl. 7, Fig. 1

Description. Leaf, blade attachment marginal, length 54 mm, width 53 mm, size notophyll, L : W ratio about 1 : 1, shape ovate, medially symmetric, base symmetric; margin untoothed; apex angle obtuse, apex shape rounded, base angle obtuse, base shape cordate. Primary venation basal actinodromous, with three basal veins, simple agrophic veins present. Major secondary venation brochidodromous, major secondary vein spacing irregular, variation of major secondary angle to midvein uniform, major secondary vein attachment to midvein excurrent. Tertiary veins opposite percurrent, with a straight course.

Remarks. *Dicotylophyllum* sp. 13 is characterised by an untoothed margin, an ovate lamina, and a cordate base. Cordate

bases are uncommon within the Morrin Bridge assemblage and serve to differentiate this leaf from other taxa present. However, because this fossil-taxon is represented by a single specimen, more precise taxonomic placement is precluded.

***Dicotylophyllum* sp. 14**

Pl. 7, Fig. 2

Description. Leaf fragmentary, petiolate, blade attachment marginal, preserved length about 29 mm, preserved width about 44 mm, size microphyll, laminar L : W ratio about 0.66 : 1, laminar shape ovate, medially symmetric, base symmetric; margin untoothed, lobed; apex angle acute, apex shape straight, base angle obtuse, base shape truncate. Primary venation basal actinodromous, with four basal veins. Major secondary veins poorly preserved.

Remarks. *Dicotylophyllum* sp. 14 is characterised by a four-lobed lamina, an untoothed margin, basal actinodromous venation, and a robust petiole. Leaf lobing typically involves odd numbers of lobes, three-, five-, and seven-lobed leaves are the most common. Curiously, *Dicotylophyllum* sp. 14 has an even number of lobes, and does not have a central lobe.

***Dicotylophyllum* sp. 15**

Pl. 7, Fig. 3

Description. Leaf fragmentary, petiolate, blade attachment marginal, preserved length about 59 mm, preserved width about 41 mm, preserved size notophyll, shape appears ovate; weakly lobed, margin toothed, serrate; base angle obtuse, base shape appears rounded or truncate. Primary venation basal actinodromous, with at least four basal veins, simple agrophic veins present. Major secondary venation craspedodromous. Tooth spacing regular, with two orders of teeth, 2 to 3 teeth per centimeter, sinus shape rounded, tooth shape concave-convex.

Remarks. *Dicotylophyllum* sp. 15 is represented by a leaf with evenly spaced compound teeth bearing rounded apices and shallow, weakly developed lobes. Unlike other lobed taxa in the Morrin Bridge assemblage *Dicotylophyllum* sp. 15 is distinctly toothed.

***Dicotylophyllum* sp. 16**

Pl. 7, Fig. 4

Description. Leaf fragmentary, petiolate, blade attachment marginal, preserved length about 58 mm, preserved width about 93 mm, laminar size mesophyll, laminar shape appears ovate; lobed, margin untoothed; apex angle acute, apex shape rounded, base angle obtuse, base shape lobate. Primary venation basal actinodromous, with five basal veins. Major secondary venation brochidodromous.

Remarks. The lobes of *Dicotylophyllum* sp. 16, particularly the central one, appear malformed—potentially due to insect damage sustained early in the leaf's development. The primary venation appears basal actinodromous, but palinactinodromous venation is also possible given the malformation

of the leaf. The specimen shares morphological characters consistent with leaves assigned to the Upper Cretaceous fossil-genus *Araliaephyllum* FONTAINE, notably a palmate lobed lamina, basal actinodromous or palinactinodromous venation, untoothed margins, and brochidodromous secondary veins. However, because only a single specimen exhibiting apparent malformation is available, such an assignment is not made at this time.

***Dicotylophyllum* sp. 17**

Pl. 7, Fig. 5

Description. Leaf fragmentary, preserved length about 103 mm, preserved width about 114 mm, preserved size mesophyll, laminar shape appears ovate; lobed, margin untoothed. Primary venation appears basal actinodromous.

Remarks. *Dicotylophyllum* sp. 17 appears to be a three-lobed leaf; however, due to damage, it is possible that it was originally five-lobed. A small incipient lobe on the left side of the lamina supports this possibility. The overall shape of this leaf is similar to leaves typically attributed to the Platanaceae. However, the limited preservation makes it difficult to confidently assign it to that family. The primary venation appears to be basal actinodromous or possibly palinactinodromous, with three or four basal veins, but damage to the leaf base precludes a definitive determination. Secondary venation is not visible, which may be due to preservation, or it may reflect weakly developed secondary veins that were not strongly impressed during fossilisation.

Genus *Carpolithes* BRONGN.

***Carpolithes* sp. 1**

Pl. 7, Fig. 6

Description. Seed, elliptic, flattened, 9 mm long, 6.8 mm wide, margin entire. Distinct median line or fissure, straight to slightly curved, extending longitudinally.

Remarks. *Carpolithes* sp. 1 consists of a single seed displaying a narrow suture or fissure running longitudinally along its centre.

***Carpolithes* sp. 2**

Pl. 7, Fig. 7

Description. Seeds, orbicular to suborbicular, flattened, about 5 mm long, about 4 to 5 mm wide, margin entire.

Remarks. *Carpolithes* sp. 2 consists of a cluster or aggregation of small, rounded seeds or fruits. The grouping lacks distinct organisation or symmetry, and the individual units are closely packed without a clear arrangement.

***Carpolithes* sp. 3**

Pl. 7, Fig. 8

Description. Seed, fragmentary, 6.2 mm long, 8 mm wide, margin entire.

Remarks. *Carpolithes* sp. 3 represents a fragmentary section of a seed or fruit. The interior appears hollow or unfilled, possibly due to original structure or preservation, and the walls are relatively thin.

***Carpolithes* sp. 4**

Pl. 7, Fig. 9

Description. Fruit (?), ovate, 10.2 mm long, 7 mm wide, apex appears acute, base rounded, margin entire. Seed central, oval to orbicular, distinct from surrounding endocarp; white layer present, possibly exocarp.

Remarks. *Carpolithes* sp. 4 appears to be a fruit. The seed is visible at the centre and delineated from the surrounding endocarp, there is a white layer which could be the exocarp. The fruit is teardrop-shaped while the seed is oval to circular in shape. It is possible this fruit could belong to *Ginkgo*, as fruits of similar morphology are commonly found in the Upper Cretaceous deposits of Alberta and are typically attributed to the Ginkgoaceae (Bell 1949).

Unidentified seeds

Pl. 7, Fig. 10

Description. Seeds, clustered, about 1.7 mm long, about 2 mm wide, ovate to orbicular, possibly winged.

Remarks. These specimens represent a compact cluster of what appear to be small, circular, winged seeds preserved in close association. It is unclear whether the seeds were originally part of a larger unified structure, such as an infructescence, or became aggregated after being dispersed from a parent structure or flower. Seed clusters, or aggregations, of this kind are common within the Morrin Bridge fossil flora.

Unidentified floral structure

Pl. 7, Fig. 11

Description. Floral structure (?), 16 mm in diameter, darkened central disk surrounded by five petals (?), each petal is 3 to 5 mm long and 4 to 6 mm wide.

Remarks. This specimen appears to be a floral structure, characterised by five small petals surrounding a darkened central disc. No other structures or diagnostic features are preserved in this enigmatic fossil.

Palaeoclimate and palaeoenvironment results

CLAMP analysis of the fossil leaf assemblage yielded a MAT of $12.2 (\pm 2.1) ^\circ\text{C}$, and MAT from LMA was estimated at $12.6 (\pm 3.0) ^\circ\text{C}$. MAT from the ensemble analysis was estimated at $12.4 (\pm 2.7) ^\circ\text{C}$. WQT was estimated at $20.0 (\pm 2.5) ^\circ\text{C}$, and CQT at $3.8 (\pm 3.2) ^\circ\text{C}$. MAXT was estimated at $26.1 (\pm 3.3) ^\circ\text{C}$ and MINT was estimated at $-1.3 (\pm 3.9) ^\circ\text{C}$. MAP from CLAMP was reconstructed at $1245 (-409/+610) \text{ mm}\cdot\text{yr}^{-1}$, and $1300 (-390/+560) \text{ mm}\cdot\text{yr}^{-1}$ from LAA. The

ensemble MAP was $1282 (-405/+585) \text{ mm}\cdot\text{yr}^{-1}$. WMP was estimated at $155 (-57/+90) \text{ mm}$, while DMP was $71 (-39/+90) \text{ mm}$. RH was estimated at $81.8 (\pm 9.3) \%$ and NPP at $674 (398-1023) \text{ gC}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

The results of the closest climatic analogue analysis indicate that the Morrin Bridge region had the strongest climatic similarities to regions that have temperate oceanic climates (Cfb) and border with warm-summer humid continental climates (Dfb) with some marine moderation, such as Southern France, the Balkans, the Black Sea, and southeast United States (Text-fig. 2). The close climatic analogues consistently lack precipitation seasonality, but are in, or border on, areas with hot summers (Cfa, Dfa). Morrin Bridge today is also in a warm-summer humid continental climate, but fringes on a cold summer (Dfc) climate to the northwest and cold steppe (BSk) to the southeast (Beck et al. 2018).

The results from the Whittaker Biome analysis indicate that the Morrin Bridge fossil flora plots within the temperate seasonal forest biome on the Whittaker diagram, though the error margins also allow for placement within the woodland/shrubland biome (Text-fig. 3).

Discussion

Despite the abundance of fossil plant material preserved in the Horseshoe Canyon Formation (HCF), the macrofloral record of this unit has received comparatively little systematic study. Most previous work on Upper Cretaceous macrofloras from Western Canada has focused either on isolated taxa or silicified mesofloral assemblages (e.g., Serbet and Stockey 1991, Serbet and Rothwell 2003, Serbet et al. 2013), whereas broader surveys of the macroflora assemblages remain rare (e.g., McIver 2002, Bamforth et al. 2014). The studies by McIver (2002) and Bamforth et al. (2014) were based on uppermost Maastrichtian macrofloras stratigraphically just below the K-Pg boundary and were focused on palaeoenvironmental reconstruction so provided little detail about the full plant fossil assemblages. Demers-Potvin and Larsson (2019) provided a palaeoclimate reconstruction based on a Cenomanian angiosperm leaf assemblage from Eastern Canada, but similar to the two studies from Saskatchewan did not describe the macrofloral assemblage. Additional studies of Upper Cretaceous macrofloras from British Columbia (e.g., Pearson and Hebda 2006, Jonsson and Hebda 2015, Greenwood et al. 2022) represent floras on rafted terranes that were likely well south of their current latitude. As a result, our understanding of Late Cretaceous vegetation in Western Canada, proximal to the Western Interior Seaway, particularly in comparison to the extensively studied floras of the Western Interior of the United States (e.g., Wolfe and Upchurch Jr. 1986, 1987, Johnson 1996, 2002, Johnson et al. 2003, Wilf and Johnson 2004, Peppe et al. 2007, Arens and Allen 2014, Deibel et al. 2024), remains limited. The Morrin Bridge locality helps fill this knowledge gap by providing new insights into the composition and structure of early Maastrichtian plant communities in Alberta.

The Morrin Bridge early Maastrichtian macroflora

The Morrin Bridge assemblage records a diverse Upper Cretaceous plant community in which gymnosperms, although represented by fewer taxa (22) than angiosperms (34) and sporing plants (2), dominate the flora in terms of specimen abundance. This reflects the prevalence of conifer foliage and cone organs in the deposit, even if several of these organs likely represent the same biological species. Cupressaceae are particularly diverse, represented by several ovuliferous and pollen cone taxa, many resembling Sequoioideae such as *Sequoia*, *Metasequoia*, and the fossil-genus *Drumhelleria*. Ginkgophytes are represented by the taxa *Ginkgoites* sp., *Ginkgoites pluripartitus*, and *Baiera*. Cycadophytes are present with two taxa that are similar to foliage typically assigned to *Pterophyllum*, as well as *Nilssonia serotina*. Sporing plants are rare, with only a single *Equisetum* root and one other fern fragment of uncertain affinity identified.

Although angiosperms are less abundant than gymnosperms at Morrin Bridge by specimen number, they are taxonomically diverse. Monocots are represented by two species of *Monocotyllophyllum*. Among dicots, Platanaceae leaves are present, particularly *Platanites marginatus*, forms resembling *Pseudoprotophyllum*, and forms assignable to *Platanophyllum*. Other notable angiosperms include *Trochodendroides arctica* (Cercidiphyllaceae), *Zizyphoides flabella* (Trochodendraceae), and a member of the Betulaceae. Seventeen of the twenty-four broadleaf dicots remain taxonomically uncertain but exhibit a range of leaf shapes, margins, and venation types, including toothed, untoothed, and lobed forms. Fruit and reproductive structures were also recovered, including the fruit *Jenkinsella arctica* (Cercidiphyllaceae), cf. *Platananthus* (Platanaceae), a flower, seed clusters, and a variety of *Carpolithes* taxa.

The flora from the Morrin Bridge locality within the upper Horsethief Member of the HCF provides a valuable point of comparison to the earlier described Upper Cretaceous 'Lower Edmonton Formation', now the Edmonton Group of which the HCF is the basal most unit, flora of Bell (1949). Notably, Bell's (1949) flora was compiled from multiple localities and encompasses a broad sampling of the lower HCF but is less rich than the single locality flora of Morrin Bridge, which suggests that the lower angiosperm diversity reported in Bell's study reflects either taxonomic oversimplification, where distinct leaf types may have been lumped into broadly defined taxa, or that the floras he examined were simply less diverse than the Morrin Bridge flora. Bell's (1949) assemblage includes *Equisetum perlaevigatum*, *Nilssonia* spp., *N. serotina*, *Ginkgoites* sp., *Carpolithes* (*Ginkgoites*?) *fultonii* W.A.BELL and *C. (Ginkgoites?) kneehillensis* W.A.BELL, *Torreyites tyrrellii*, *Cunninghamiostrobus*? sp., *Sequoiites artus*, *Sequoiites dakotensis* (R.W.BR.) W.A.BELL, *Elatocladus intermedius*, *Thuites interruptus*, *Juniperites gracilis*, *Dombeyopsis nebrascensis* (NEWB.) W.A.BELL, *Nymphaeites angulatus* (NEWB.) W.A.BELL, *Vitis stantonii* (KNOWLTON) R.W.BR., *Trochodendroides arctica*, and *Jenkinsella arctica*, many of which are also present or represented by closely comparable taxa at Morrin Bridge.

Morrin Bridge preserves *Equisetum*, a broader diversity of Ginkgophyta, including *Baiera* and two fossil-species of *Ginkgoites*, three Cycadophytes including *Nilssonia serotina*, as well as an expanded conifer record with multiple

Cupressaceae cones and foliage types, some of which resemble Bell's (1949) figured *Sequoiites*. We acknowledge the similarity of *Elatocladus* var. A and C to *Sequoiites artus*, but we could not confidently assign them. Bell (1949) described Sequoioideae ovuliferous cones as *Sequoiites dakotensis*. While the ovuliferous complexes are peltate and helically arranged, like in unidentified Sequoioideae ovuliferous cone 1, the preservation is too different from the Morrin Bridge fossils to achieve a meaningful comparison. Cones comparable to Bell's (1949) *Pityostrobus* (*Cunninghamiostrobus*?) sp. were not recovered from the Morrin Bridge locality. In terms of pollen cone branches, the Morrin Bridge flora yielded fossils assignable to *Taxodium* and suspected *Drumhelleria*. Bell's (1949) flora includes one incompletely preserved shoot (*Juniperites gracilis*) that looks morphologically similar to *Drumhelleria* pollen cone branches (Bell 1949: pl. 4, fig. 5) and is in need of reinvestigation.

The Morrin Bridge flora as well as Bell's (1949) Lower Edmonton Formation flora both include the foliage type *Cupressinocladus interruptus* and fossil leaves and leafy shoots assigned to the form genus *Torreyites* (Bell 1949). Bell (1949) did not describe any fossils similar to the morphologically diverse shoots of *Pagiophyllum* from the Lower Edmonton Formation. The only macromorphologically comparable fossil-species, *Cryptomerites lambii* from Paleocene beds overlying the Cretaceous Brazeau Formation and from the Paskapoo Formation, requires revision.

Bell's (1949) flora includes the angiosperm taxa *Dombeyopsis nebrascensis*, *Nymphaeites angulatus*, and *Vitis stantonii*, these are absent at Morrin Bridge; however, some of the *Vitis stantonii* leaves figured by Bell (1949: pl. 9, Fig. 5), may be misidentified and could instead represent Platanaceae leaves, especially as these leaves have palinactinodromous basal venation typical of Platanaceae leaves and lack the cordate base typically seen in *Vitis stantonii* (Arens and Allens 2014).

Dombeyopsis nebrascensis was a new combination by Bell that included leaves previously recognised as *Trochodendroides*, but also leaves assigned to "*Populus*" *nebrascensis* that included a variety of forms from different taxa (see Bell 1949). Many of Bell's *D. nebrascensis* leaves were later transferred into *Archeampelos acerifolia* by McIver and Basinger (1993). It is likely that Bell's concept of *D. nebrascensis* was artificial as it included multiple leaf forms, some of which are present at Morrin Bridge within the Cercidiphyllaceae (i.e., *Trochodendroides* and *Archeampelos*) and Trochodendraceae leaf taxa, particularly given the close morphological overlap between fossil leaves from these two families. Bell (1949) suggested leaves of *Nymphaeites angulatus* were part of the Nymphaeaceae; however, McIver and Basinger (1993) later transferred these into the newly established fossil-genus *Trapago* McIVER et BASINGER, which is considered a junior synonym of the fossil-genus *Quereuxia* KRYSHT. in BAIKOVSKAJA (Hickey 2001). These aquatic plants are well-known from Upper Cretaceous deposits in Alberta (Bell 1949, Stockey and Rothwell 1997), and their absence from Morrin Bridge suggests the depositional environment (a fluvial system or crevasse splay) may not have been suitable for their growth.

The Morrin Bridge locality yields a richer and more compositionally distinct angiosperm component than the floras studied by Bell (1949), despite the latter having been

compiled from multiple localities. The Morrin Bridge assemblage includes Platanaceae (*Platanites*, *Pseudoprotophyllum*, *Platanophyllum*), members of the Cercidiphyllaceae (*Trochodendroides*, *Archeampelos*, *Jenkinsella*), a member of the Betulaceae (*Corylites*), trochodendroids (*Zizyphoides flabella*), and monocots (*Monocotylrophyllum* spp.). This diversity, captured from a single site, underscores both regional variability and the influence of localised environmental and preservational conditions.

Many of the taxa identified in the Morrin Bridge fossil flora, or their close equivalents, are also documented in other Upper Cretaceous floras across North America. *Pterophyllum* has been reported from Upper Cretaceous deposits in Alaska (Hollick 1930), while *Nilssonina* is widespread in Upper Cretaceous strata throughout the continent (Hollick 1930, Johnson 2002, Peppe et al. 2007). For conifers, *Cupressinocladus interruptus* is known from the Hell Creek Formation (Johnson 2002, Arens and Allen 2014). The morphologically comparable *Mesocyparis borealis* is known from the Upper Cretaceous Fox Hills Formation of North Dakota (Peppe et al. 2007). Vegetative shoots with needle-like foliage are common elements in Maastrichtian northern North American fossil assemblages, e.g., *Glyptostrobus specialis* HOLICK (Alaska: Hollick 1930), *Glyptostrobus europaeus* (BRONGN.) HEER (Hell Creek Formation: Johnson 2002, Arens and Allen 2014). Several angiosperm taxa identified at Morrin Bridge also have parallels in the Hell Creek Formation, including *Corylites*, *Zizyphoides flabella*, *Trochodendroides*, *Jenkinsella arctica*, *Platanites marginatus*, and *Platanophyllum* (Johnson 2002, Arens and Allen 2014). These comparisons suggest some regional continuity in floristic composition during the late Maastrichtian and emphasise the biogeographic relevance of the Morrin Bridge assemblage.

The composition of the Morrin Bridge macroflora corresponds broadly with the palynological data reported for the Horsethief Member. Eberth and Braman (2012) document a palynological assemblage composed of 61.2 % gymnosperm pollen, 19.6 % spores (primarily pteridophytes), and only 16.7 % angiosperm pollen. This distribution aligns with the macrofloral record from Morrin Bridge, which is dominated by gymnosperms, particularly Cupressaceae, with a lower representation of Ginkgophyta, 'Cycadophyta', and angiosperm leaves and only rare occurrences of ferns and horsetails. While taphonomic and ecological factors may influence differential preservation between pollen and leaves, the proportional underrepresentation of angiosperms in both datasets suggests that gymnosperms remained dominant in the regional vegetation during the early Maastrichtian, despite the ongoing diversification of flowering plants elsewhere in the Late Cretaceous Western Interior (Wolfe 1975, Crabtree 1987, Crane and Lidgard 1989, Graham 1993, Askin and Spicer 1995, Lupia et al. 2000, Herman 2002, Johnson 2002, Coiffard and Gomez 2010).

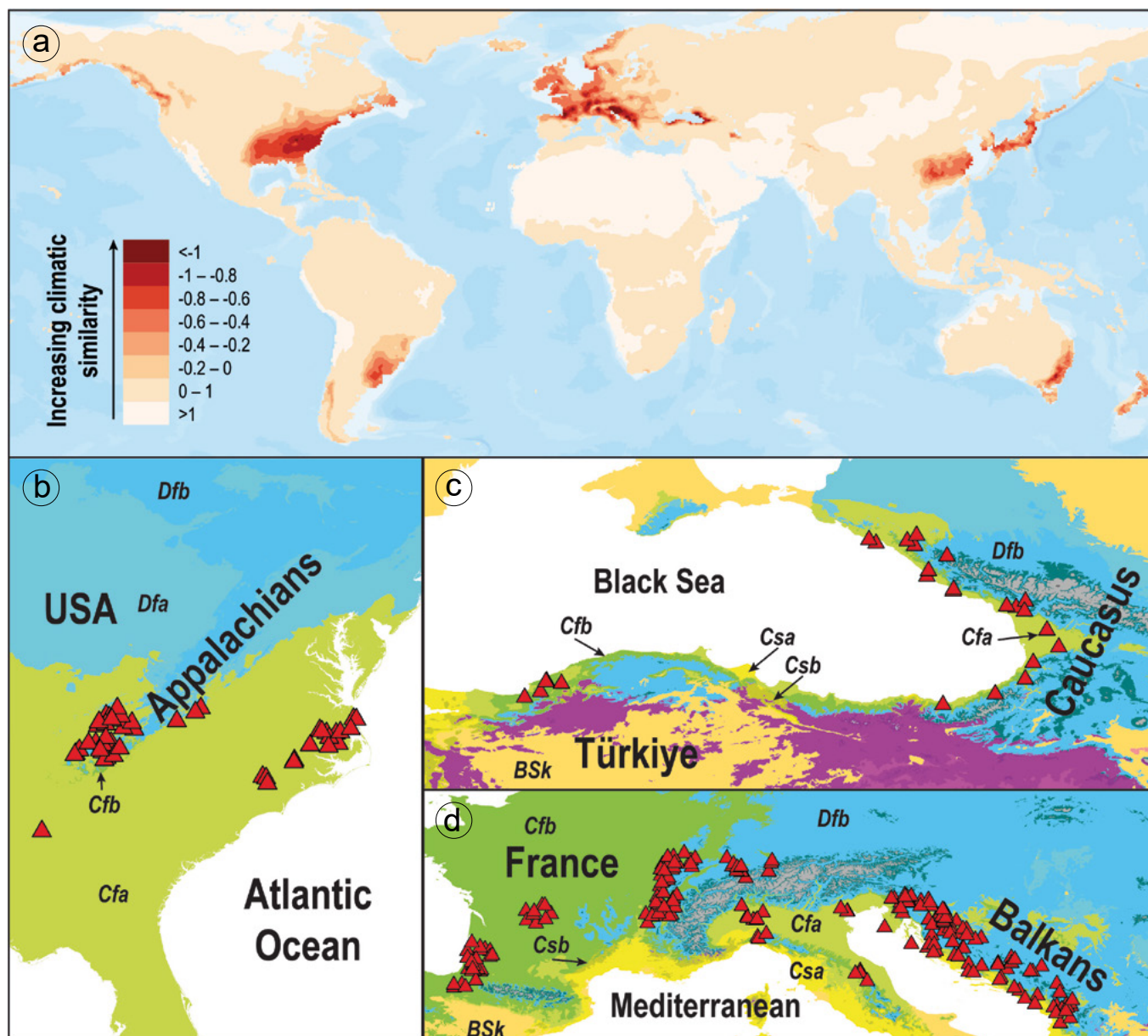
The Morrin Bridge early Maastrichtian palaeoclimate

The reconstructed temperatures – MAT of 12.4 °C (± 2.7 °C), MAXT of 26.1 °C (± 3.3 °C), and MINT of -1.3 °C (± 3.9 °C) – are consistent with a warm-temperate

climate (Tab. 2) and comparable to those of modern humid temperate zones. Based on our climate reconstruction the region was likely characterised by a growing season with warm summers and winters that were cool but remained above freezing for much of the coldest months. The relatively narrow spread between summer and winter temperatures (WQT: 20.0 ± 2.5 °C; CQT: 3.8 ± 3.2 °C) suggests minor to moderate seasonality, likely influenced by proximity to the Western Interior Seaway. This interpretation is further supported by the closest climatic analogue analysis (Text-fig. 2), which shows strong similarity to modern regions with temperate oceanic (Cfb) climates and to warm-summer humid continental (Dfb) climates, particularly those bordering Cfb zones and receiving some influence from proximity to marine conditions. Modern analogues of such climates include central and southwestern France, the Balkans, the Black Sea coastlines, and southeastern United States (Text-fig. 2). These regions are unified by their relatively mild thermal regimes with minor to moderate temperature seasonality, limited precipitation seasonality, and the absence of prolonged freezing temperatures, conditions that align closely with the reconstructed palaeoclimate for Morrin Bridge. The high MAP of 1282 ($-405/+585$) mm·yr⁻¹, alongside wettest month precipitation of 155 ($-57/+90$) mm and driest month precipitation of 71 ($-39/+90$) mm, indicates a consistently moist climate, likely lacking a severe dry season, although some precipitation seasonality is indicated. The high relative humidity (81.8 ± 9.3 %) further supports the interpretation of a humid environment. These conditions are consistent with the interpretation by Eberth and Braman (2012) from sedimentological evidence that the abundance of coals found in the Horsethief Member is indicative of saturated landscapes and relatively high water-tables.

Eberth and Braman (2012) reported an increase in palaeochannel thickness and percentage near the top of the Horsethief Member, which correlates to the relative stratigraphic position of the fossil flora. This increase in palaeochannels may reflect a shift toward higher fluvial discharge and hydrologic energy, consistent with the warm and humid palaeoclimate reconstructed from the Morrin Bridge fossil flora. Such a climate, coupled with abundant rainfall, likely would have supported increased runoff and a greater capacity for channel incision and sediment transport, contributing to the development of thicker and more frequent fluvial channel deposits in the uppermost Horsethief succession. The top of the Horsethief Member represents the end of the first coal-dominant phase in the HCF and marks the transition point toward a trend of cooler temperatures and increased seasonal dryness, as seen in the generally non-coaly deposits of the Morrin Member (Eberth and Braman 2012). This transition is also reflected in a decrease in overall sediment grain size and palaeochannel dimensions within the Morrin Member, consistent with reduced fluvial energy and a shift in regional climatic and possibly tectonic conditions (Eberth and Braman 2012, Eberth and Kamo 2020).

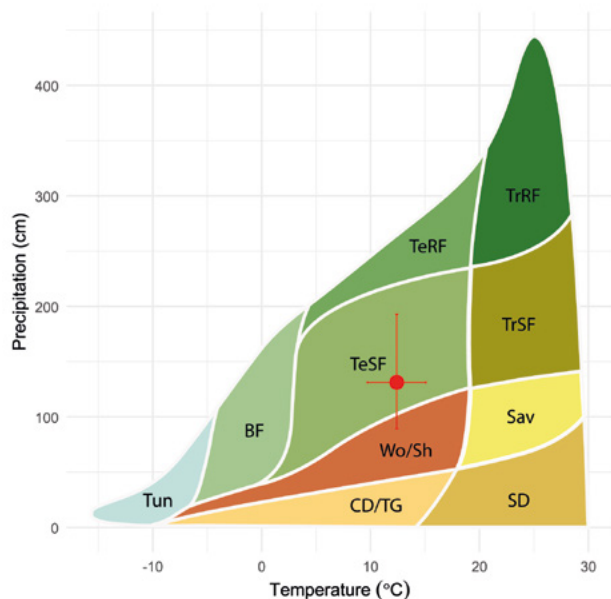
Quinney et al. (2013) conducted a detailed analysis of palaeosols across the HCF, using the five stratigraphic units established by Eberth (2004). The upper portion of Unit 1, as defined by Eberth (2004), is equivalent to the Horsethief Member of Eberth and Braman (2012), from which the Morrin Bridge fossil flora was collected. Quinney



Text-fig. 2. Closest climatic analogue analysis diagram. **a:** results of the closest climatic analogue analysis for the reconstructed Morrin Bridge palaeoclimate where dark reds indicate greater similarity and lighter pinks indicate greater dissimilarity, **b:** climatic similarity of the Morrin Bridge palaeoclimate in the southeast United States, **c:** climatic similarity of the Morrin Bridge palaeoclimate in the Black Sea region, **d:** climatic similarity of the Morrin Bridge palaeoclimate in Southern France and the Balkans. Morrin bridge represented by red triangles in panels (b), (c), and (d). BSk – cold semi-arid climate, Cfa – humid subtropical climate, Cfb – temperate oceanic climate, Csa – hot-summer Mediterranean climate, Csb – warm-summer Mediterranean climate, Dfa – hot-summer humid continental climate, Dfb – warm-summer humid continental climate.

et al. (2013) found that Unit 1 was dominated by poorly drained palaeoenvironments, with high but fluctuating water tables and only rare development of well-drained soils. A single well-drained palaeosol near the top of Unit 1 marks the beginning of a shift in drainage conditions just prior to the lithological transition at the Unit 1/Unit 2 boundary (Quinney et al. 2013). Although limited in number, the well-drained palaeosols preserved in Unit 1 suggest warm and humid climatic conditions, with a mean annual temperature of approximately $11 \pm 4.4^\circ\text{C}$ and mean annual precipitation of about 964 ± 181 mm/year (Quinney et al. 2013). The palaeoclimate reconstruction from the present study based on the Morrin Bridge fossil flora offers broadly consistent estimates to those found by Quinney et

al. (2013). When error is considered, our MAP estimates overlap with those of Quinney et al. (2013); however, overall our MAP estimates are higher, suggesting an even greater amount of precipitation or saturation in the landscape. The elevated precipitation and humidity values inferred from leaf physiognomy suggest a possible short-term increase in both temperature and precipitation prior to the cool and dry phase of the overlying Morrin Member, but nevertheless further support the interpretation of a poorly-drained, water-saturated landscape with only localised development of better-drained soils consistent with the findings of Quinney et al. (2013). This reinforces the interpretation of a warm temperate wet palaeoclimate with non-freezing winters across the upper Horsethief Member succession.



Text-fig. 3. Whittaker Biome diagram that shows the reconstructed biome of the Morrin Bridge fossil locality as a temperate seasonal forest based on the reconstructed palaeoclimate of this study. Tun – tundra, BF – boreal forest, Wo/Sh – woodland or shrubland, CD/TG – cold desert or temperate grassland, SAV – savanna, SD – subtropical desert, TeSF – temperate seasonal forest, TrSF – tropical seasonal forest, TeRF – temperate rainforest, TrRF – tropical rainforest.

Net primary productivity (NPP) at Morrin Bridge was estimated at $674 \text{ gC}\cdot\text{m}^{-2} \text{ yr}^{-1}$, with an uncertainty range of $398\text{--}1,023 \text{ gC}\cdot\text{m}^{-2} \text{ yr}^{-1}$. The central estimate aligns with the modern temperate seasonal forest biome (i.e., $631\text{--}1,040 \text{ gC}\cdot\text{m}^{-2} \text{ yr}^{-1}$), while the lower end of the range overlaps with values characteristic of woodland/shrubland biomes (i.e., $358\text{--}821 \text{ gC}\cdot\text{m}^{-2} \text{ yr}^{-1}$) (Reichgelt and West 2025). This suggests the reconstructed environment was most likely a temperate seasonal forest, though a less productive woodland cannot be excluded given the range of uncertainty. This estimate aligns with the Whittaker Biome plot (Text-fig. 3), where based on temperature and precipitation estimates Morrin Bridge plotted as a temperate seasonal forest but with error also includes a woodland/shrubland biome. These results are further supported by the closest climatic analogue analysis (Text-fig. 2), which identifies modern regions characterised by temperate deciduous forests and woodlands, mixed temperate forests composed of both broadleaf and coniferous species, and temperate rainforests (Lebourgeois et al. 2010, Curt et al. 2011, Kirkpatrick and DellaSala 2011, Box and Fujiwara 2015, Čarni 2017, Nayim 2017, Loidi et al. 2020). This pattern implies that the Morrin Bridge palaeoforest may have existed near the ecological threshold between more closed, mesic temperate forest systems and slightly more open, lower-productivity woodlands.

Bamforth et al. (2014) provided CLAMP based palaeoclimate estimates for two Maastrichtian sites from Saskatchewan, Canada. Despite their two sites, Chambéry Coulee and Grasslands National Park (GNP), being slightly younger than our flora from Morrin Bridge, their CLAMP-based palaeoclimate estimates (Tab. 2) remain valuable for comparative purposes.

MAT at Chambéry Coulee was $12.1 \pm 2.1 \text{ }^{\circ}\text{C}$, similar to our estimate of $12.4 \pm 2.7 \text{ }^{\circ}\text{C}$ for Morrin Bridge. The MAT for GNP was $14.4 \pm 2.1 \text{ }^{\circ}\text{C}$, warmer than our estimate for Morrin Bridge.

Although the variables are not directly equivalent, we can compare the warm month mean temperature (WMMT) and cold month mean temperature (CMMT) of Bamforth et al. (2014) with our WQT and CQT temperatures. WMMT and CMMT for Chambéry Coulee were $20.7 \pm 2.5 \text{ }^{\circ}\text{C}$ and $5.1 \pm 3.4 \text{ }^{\circ}\text{C}$, and for GNP were $22.5 \pm 2.5 \text{ }^{\circ}\text{C}$ and $6.7 \pm 3.4 \text{ }^{\circ}\text{C}$. Although comparable to our WQT estimate of $20.0 \pm 2.5 \text{ }^{\circ}\text{C}$ and CQT estimate of $3.8 \pm 3.2 \text{ }^{\circ}\text{C}$, the lower CQT value, which represents an average over three months rather than a single cold-month mean temperature, indicates a greater degree of seasonality at Morrin Bridge than at the Saskatchewan sites.

Bamforth et al. (2014) also provided estimates of the three wettest months (3WET) and three driest months (3DRY) for each site. These values are not directly comparable to our WMP and DMP estimates, which are for the single wettest or driest month, but dividing the 3WET and 3DRY values by three allows a rough comparison. The 3WET values for Chambéry Coulee and GNP were $617 \pm 229 \text{ mm}$ and $626 \pm 229 \text{ mm}$, respectively, yielding median monthly values of 205 mm and 208 mm for the three-month interval – wetter than our WMP estimate of 155 mm . Similarly, the 3DRY values for Chambéry Coulee and GNP were $141 \pm 59 \text{ mm}$ and $160 \pm 59 \text{ mm}$, respectively, corresponding to median monthly values of 47 mm and 53 mm . These are drier than our DMP estimate of 71 mm , suggesting that the sites in Saskatchewan were more seasonal than the Morrin Bridge site in Alberta.

Bamforth et al. (2014) did not estimate MAP from CLAMP or from LAA, so our MAP value cannot be directly compared. However, their CLAMP analysis did provide an estimate of growing season precipitation (GSP), which was $1120 \pm 317 \text{ mm}$ for Chambéry Coulee and $1,169 \pm 317 \text{ mm}$ for GNP. Although these values are lower than our MAP estimate of $1282 (-405/+585) \text{ mm}$, GSP represents only the growing season and excludes precipitation from the rest of the year. When annual totals are considered, both Chambéry Coulee and GNP were likely wetter than Morrin Bridge.

Relative humidity (RH) at Chambéry Coulee was $64.1 \pm 8.6 \%$ and at GNP was $69.6 \pm 8.6 \%$, both lower than our RH estimate of $81.8 \pm 9.3 \%$ for Morrin Bridge. This suggests that, although Chambéry Coulee and GNP were likely overall wetter sites due to higher MAP, their average humidity was substantially lower than at Morrin Bridge. Taken together, these comparisons indicate that the Chambéry Coulee and GNP sites in Saskatchewan experienced broadly similar overall warmth to Morrin Bridge but with differences in temperature seasonality as well as precipitation amount, distribution, and relative humidity. The lower RH values despite higher MAP suggest differences in precipitation seasonality across sites. These differences may reflect regional climatic patterns during the Maastrichtian but could also be related to a broader cooling trend during the Maastrichtian (Wilf et al. 2003, Friedrich et al. 2009, Thibault et al. 2016).

The Morrin Bridge macrofloral assemblage thus offers a well-collected ($n \approx 890$ specimens) and compositionally rich macrofloral record from a single quarry sampling a single stratigraphic horizon from the upper Horseshoe Member, capturing the structure and diversity of a warm-temperate, humid

ecosystem in the early Maastrichtian of Alberta. The taxonomic overlap with Bell's (1949) Lower Edmonton Formation flora, alongside notable differences in diversity and preservation, emphasises the importance of localised environmental and taphonomic factors. When considered alongside the palynological, sedimentological, and palaeopedological data from the Horseshoe Canyon Formation (i.e., Eberth and Braman 2012, Quinney et al. 2013), the Morrin Bridge flora adds resolution to the understanding of vegetational heterogeneity and landscape hydrology near the end of the Cretaceous period. The placement of the Morrin Bridge fossil flora within a mosaic of mixed forest and woodland vegetation under a warm, perennially moist climate reinforces the significance of this locality as a reference point for reconstructing Late Cretaceous plant communities and palaeoclimate, similar to the Maastrichtian sites from Saskatchewan (Bamforth et al. 2014), in the Western Interior.

Conclusions

The fossil flora from the Morrin Bridge locality provides a detailed window into early Maastrichtian vegetation and climate in Western Canada, at a time of both regional environmental transition and global ecological change. Sampled from the uppermost part of the Horseshoe Member of the Horseshoe Canyon Formation, this assemblage preserves a diverse array of plant fossils, including gymnosperms, angiosperms, and sporing plants. Gymnosperms dominate the assemblage in terms of specimen abundance, led by Cupressaceae and supplemented by 'Cycadophyta' and Ginkgophyta. While angiosperms are less abundant than the conifers found at the site, they are taxonomically diverse, with representatives of Platanaceae, Cercidiphyllaceae, Trochodendraceae, Betulaceae, and multiple dicots that remain taxonomically uncertain but morphologically distinct.

Palaeoclimate estimates based on leaf physiognomy indicate a warm, humid climate, with a mean annual temperature of ~12 °C, high annual precipitation (~1,282 mm·yr⁻¹) and relative humidity (~81 %). Our palaeoclimate estimates for the lower Maastrichtian Morrin Bridge flora are comparable to previously published estimates from the upper Maastrichtian Chamberly Coulee and Grasslands National Park (GNP) floras in Saskatchewan (Tab. 2), suggesting stronger temperature seasonality, lower precipitation seasonality, and higher overall humidity for the older Morrin Bridge flora. The Morrin Bridge reconstructions are consistent with prior evidence from sedimentology and palaeosol analyses and potentially support sedimentological evidence for an increase in palaeochannel thickness and frequency suggesting increased fluvial activity, driven by an enhanced hydrological system. These findings place the Morrin Bridge flora near to the transition from coal-rich, waterlogged landscapes to more dynamic, seasonally influenced fluvial systems.

The Morrin Bridge fossil flora contributes significantly to the underdeveloped macrofloral record of the Horseshoe Canyon Formation and highlights the need for further site-specific studies to fully capture the ecological variability of Late Cretaceous vegetation in Western Canada. As a relatively well collected ($n \approx 890$) and species-rich assemblage (58 taxa) sampled from a single quarry and stratigraphic horizon, the

Morrin Bridge locality offers opportunities for refining regional palaeoecological reconstructions and for understanding the composition of Late Cretaceous vegetation in Alberta in the lead up to the K-Pg extinction event.

Acknowledgements

Alfred Lemierre, Mark Mitchell, Kano Sasaguchi, Parker Senger, and Urgan Snider are thanked for their assistance in the field. Dennis Braman is thanked for thoughtful discussions on the stratigraphy of the Morrin Bridge area and for making the initial collection of fossils. This research was in part funded by the Austrian Science Fund (FWF) 10.55776/PAT2207723 (LJS and KH). DRG's contribution was made possible by a research grant from the Natural Sciences and Engineering Research Council of Canada (RGPIN 2016-04337). We also thank two anonymous reviewers for their helpful suggestions that improved the original manuscript.

References

- Andruchow-Colombo, A., Andruchow, M. S., Bodnar, J., Passalia, M. G. (2022): New genus of Cupressaceae from the Upper Cretaceous of Patagonia (Argentina) fills gap in the evolution of the ovuliferous complex in the family. – *Journal of Systematics and Evolution*, 60: 1417–1439. <https://doi.org/10.1111/jse.12842>
- Arens, N. C., Allen, S. E. (2014): A florule from the base of the Hell Creek Formation in the type area of eastern Montana: Implications for vegetation and climate. – *Geological Society of America, Special Paper*, 503: 173–207. [https://doi.org/10.1130/2014.2503\(06\)](https://doi.org/10.1130/2014.2503(06))
- Arnold, C. A., Lowther, J. S. (1955): A new Cretaceous conifer from Northern Alaska. – *American Journal of Botany*, 42: 522–528. <https://doi.org/10.1002/j.1537-2197.1955.tb11156.x>
- Askin, R. A., Spicer, R. A. (1995): The Late Cretaceous and Cenozoic history of vegetation and climate at northern and southern high latitudes: A comparison. – In: *National Research Council (US) Panel on Effects of Past Global Change on Life, Effects of Past Global Change on Life*. National Academies Press, Washington, D.C., pp. 22–25.
- Aulenback, K. R. (2009): Identification Guide to the Fossil Plants of the Horseshoe Canyon Formation of Drumheller, Alberta. – University of Calgary Press, Alberta. <https://doi.org/10.1515/9781552384947>
- Aulenback, K. R., Braman, D. R. (1991): A chemical extraction technique for the recovery of silicified plant remains from ironstones. – *Review of Palaeobotany and Palynology*, 70: 3–8. [https://doi.org/10.1016/0034-6667\(91\)90075-E](https://doi.org/10.1016/0034-6667(91)90075-E)
- Aulenback, K. R., LePage, B. A. (1998): *Taxodium wallisii* sp. nov.: first occurrence of *Taxodium* from the Upper Cretaceous. – *International Journal of Plant Sciences*, 159: 367–390. <https://doi.org/10.1086/297558>
- Bamforth, E. L., Button, C. L., Larsson, H. C. (2014): Paleoclimate estimates and fire ecology immediately prior to the end-Cretaceous mass extinction in the Frenchman Formation (66 Ma), Saskatchewan,

- Canada. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 401: 96–110.
<https://doi.org/10.1016/j.palaeo.2014.02.020>
- Basinger, J. F. (1981): The vegetative body of *Metasequoia milleri* from the Middle Eocene of southern British Columbia. – *Canadian Journal of Botany*, 59: 2379–2410.
<https://doi.org/10.1139/b81-291>
- Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., Wood, E. F. (2018): Present and future Köppen-Geiger climate classification maps at 1-km resolution. – *Scientific Data*, 5(1): 1–12.
<https://doi.org/10.1038/sdata.2018.214>
- Bell, W. A. (1949): Uppermost Cretaceous and Paleocene floras of western Alberta. – *Geological Survey of Canada Bulletin*, 13: 1–231.
<https://doi.org/10.4095/101514>
- Bell, W. A. (1956): Lower Cretaceous floras of western Canada. – *Geological Survey of Canada Memoir*, 285: 1–334. <https://doi.org/10.4095/101511>
- Bell, W. A. (1957): Flora of the Upper Cretaceous Nanaimo Group of Vancouver Island, British Columbia. – *Geological Survey of Canada Memoir*, 293: 1–84.
<https://doi.org/10.4095/101457>
- Bell, W. A. (1963): Upper Cretaceous floras of the Dunvegan, Bad Heart, and Milk River formations of western Canada. – *Geological Survey of Canada, Bulletin*, 94, 76 pp.
<https://doi.org/10.4095/100613>
- Bell, W. A. (1965): Illustrations of Canadian fossils: Upper Cretaceous and Paleocene plants of western Canada. – *Geological Survey of Canada, Paper*, 63(35): 1–46.
<https://doi.org/10.4095/100938>
- Bell, P. R., Campione, N. E. (2014): Taphonomy of the Danek Bonebed: a monodominant *Edmontosaurus* (Hadrosauridae) bonebed from the Horseshoe Canyon Formation, Alberta. – *Canadian Journal of Earth Sciences*, 51: 1–15.
<https://doi.org/10.1139/cjes-2014-0062>
- Berry, E. W. (1930): Fossil plants from the Cypress Hills of Alberta and Saskatchewan. – *Canada National Museum Bulletin*, 63: 15–28.
<https://doi.org/10.4095/105046>
- Berry, E. W. (1935): A preliminary contribution to the floras of the Whitemud and Ravenscrag formations. – *Geological Survey of Canada, Memoir*, 182: 1–107.
<https://doi.org/10.4095/100814>
- Braman, D. R. (2018): Terrestrial palynostratigraphy of the Upper Cretaceous (Santonian) to lowermost Paleocene of southern Alberta, Canada. – *Palynology*, 42(1): 102–147.
<https://doi.org/10.1080/01916122.2017.1311958>
- Brink, K. S., Smith, S. Y., Stockey, R. A. (2009): *Cunninghamia hornbyensis* sp. nov.: permineralized twigs from the Upper Cretaceous of Hornby Island, British Columbia, Canada. – *Review of Palaeobotany and Palynology*, 155: 89–98.
<https://doi.org/10.1016/j.revpalbo.2009.03.005>
- Bogner, J., Hoffman, G. L., Aulenback, K. R. (2005): A fossilized aroid infructescence, *Albertarum pueri* gen. nov. et sp. nov., of Late Cretaceous (Late Campanian) age from the Horseshoe Canyon Formation of southern Alberta, Canada. – *Canadian Journal of Botany*, 83(6): 591–598.
<https://doi.org/10.1139/b05-033>
- Bogner, J., Johnson, K. R., Kvaček, Z., Upchurch, G. R. (2007): New fossil leaves of Araceae from the Late Cretaceous and Paleogene of western North America. – *Zitteliana*, A, 47: 133–147.
- Boulter, M. C., Kvaček, Z. (1989): The Palaeocene flora of the Isle of Mull. – *Palaeontological Association Special Papers in Palaeontology*, 42: 1–149.
- Box, E. O., Fujiwara, K. (2014): Warm-temperate deciduous forests: concept and global overview. – In: Box, E. O., Fujiwara, K. (eds), *Warm-Temperate Deciduous Forests Around the Northern Hemisphere*. Springer, Cham, pp. 7–26. https://doi.org/10.1007/978-3-319-01261-2_2
- Brongniart, A. (1825): Observations sur les végétaux fossiles refermes dans les Gres de Hoer en Scanie. – *Annales des sciences naturelles*, 4: 200–224.
- Brongniart, A. (1828): *Prodrome d'une histoire des végétaux fossiles*. – Paris, 223 pp.
<https://doi.org/10.5962/bhl.title.62840>
- Brown, R. W. (1939): Fossil leaves, fruits, and seeds of *Cercidiphyllum*. – *Journal of Palaeontology*, 13: 485–499.
- Brown, R. W. (1962): Paleocene flora of the Rocky Mountains and great Plains. – *Geological Survey Professional Paper*, Washington, D.C., 375: 199 pp., 69 pls.
<https://doi.org/10.3133/pp375>
- Čarni, A. (2017): Vegetation of deciduous forests in the Balkan Peninsula. – *Contributions, Section of Natural, Mathematical and Biotechnical Sciences*, 37(2): 93–104.
<https://doi.org/10.20903/csnmbs.masa.2016.37.2.87>
- Capellini G., von Heer O. (1866): Les phyllites crétacées du Nebraska. – *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften*, 22(1): 1–22.
- Čepičková, J., Kvaček, J. (2020): Two cycads *Nilssonia mirovanae* sp. nov. and *Pseudoctenis babinensis* J.Kvaček from the Cenomanian of the Bohemian Cretaceous Basin (the Czech Republic) as indicators of water stress in the palaeoenvironment. – *Fossil Imprint*, 76(2): 315–324.
<https://doi.org/10.37520/fi.2020.025>
- Coiffard, C., Gomez, B. (2010): The rise to dominance of the angiosperm kingdom: dispersal, habitat widening and evolution during the Late Cretaceous of Europe. – *Lethaia*, 43(2): 164–169.
<https://doi.org/10.1111/j.1502-3931.2009.00181.x>
- Crabtree, D. R. (1987): Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. – *Annals of the Missouri Botanical Garden*, 74(4): 707–747.
<https://doi.org/10.2307/2399448>
- Crane, P. R. (1981): Betulaceous leaves and fruits from the British Upper Palaeocene. – *Botanical Journal of the Linnean Society*, 83(2): 103–136.
<https://doi.org/10.1111/j.1095-8339.1981.tb01224.x>
- Crane, P. R., Lidgard, S. (1989): Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. – *Science*, 246(4930): 675–678.
<https://doi.org/10.1126/science.246.4930.675>
- Crane, P. R., Manchester, S. R., Dilcher, D. L. (1991): Reproductive and vegetative structure of *Nordenskiöldia* (Trochodendraceae), a vesselless dicotyledon from the early Tertiary of the Northern Hemisphere. – *American*

- Journal of Botany, 78(10): 1311–1334.
<https://doi.org/10.1002/j.1537-2197.1991.tb12599.x>
- 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, 63(2): 340–364.
<https://doi.org/10.1139/b85-041>
- Curt, T., Schaffhauser, A., Borgniet, L., Dumas, C., Estève, R., Ganteaume, A., Jappiot, M., Martin, W., N'Diaye, A., Poilvet, B. (2011): Litter flammability in oak woodlands and shrublands of southeastern France. – Forest Ecology and Management, 261(12): 2214–2222.
<https://doi.org/10.1016/j.foreco.2010.12.002>
- Dawson, J. W. (1883): On the Cretaceous and Tertiary Floras of British Columbia and Northwest Territory. – Proceedings and Transactions of the Royal Society of Canada, 1(4): 15–34.
<https://doi.org/10.5962/bhl.title.38371>
- Deibel, P. K. W., Mantilla, G. P. W., Strömberg, C. A. (2024). Plant taxonomic turnover and diversity across the Cretaceous/Paleogene boundary in northeastern Montana. – Paleobiology, 50(4): 608–626.
<https://doi.org/10.1017/pab.2024.22>
- Demers-Potvin, A. V., Larsson, H. C. (2019): Palaeoclimatic reconstruction for a Cenomanian-aged angiosperm flora near Schefferville, Labrador. – Palaeontology, 62(6): 1027–1048.
<https://doi.org/10.1111/pala.12444>
- Dorf, E. (1942): Upper Cretaceous Floras of the Rocky Mountain Region II: Flora of the Lance Formation at its Type Locality, Niobrara County, Wyoming. – Carnegie Institute of Washington, Washington, 159 pp., 17 pls.
- Dörken, V. M. (2020): Cones of Conifers: Morphology, Anatomy and Functional Aspects of Coniferous Reproductive Structures. – Verlag Kessel, Kessel, 28 pp.
- Dörken, V. M., Nimsch, H. (2018): Differentialdiagnostik in Koniferen – ein illustrierter Gattungsschlüssel. – Verlag Kessel, Kessel, 186 pp.
- Doweld, A. B. (2016): (2423–2424) Proposals to conserve the names *Ullmannia*, with a conserved type, against *Anthotropolithes* and *Cupressites* and *U. bronnii* against *Anthotropolithes ranunculiformis*, *Cupressus ullmannii*, and *Cupressites bituminosus* (fossil Gymnospermae: Voltziopsida). – Taxon, 65(1): 190–191.
<https://doi.org/10.12705/651.22>
- Eberth, D. A. (2004): A revised stratigraphy for the Edmonton Group (Upper Cretaceous) and its potential sandstone reservoirs. – In: CSPG-CHOA-CWLS Joint Conference Calgary, AB, Pre-Conference Field Trip #7 guidebook. Canadian Society of Petroleum Geologists, Calgary, Alberta.
- Eberth, D. A., Bell, P. R. (2014): Stratigraphy of the Danek Bonebed (Upper Cretaceous Horseshoe Canyon Formation, central Alberta) and correlations with strata in the Drumheller and Grande Prairie regions. – Canadian Journal of Earth Sciences, 51: 975–981.
<https://doi.org/10.1139/cjes-2014-0069>
- Eberth, D. A., Braman, D. R. (2012): A revised stratigraphy and depositional history for the Horseshoe Canyon Formation (Upper Cretaceous), southern Alberta plains. – Canadian Journal of Earth Sciences, 49(9): 1053–1086.
<https://doi.org/10.1139/e2012-035>
- Eberth, D. A., Evans, D. C., Brinkman, D. B., Therrien, F., Tanke, D. H., Russell, L. S. (2013): Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climate influence. – Canadian Journal of Earth Sciences, 50(7): 701–726.
<https://doi.org/10.1139/cjes-2012-0185>
- Eberth, D. A., Kamo, S. L. (2020): High-precision U–PB CA–ID–TIMS dating and chronostratigraphy of the dinosaur-rich horseshoe canyon formation (Upper Cretaceous, Campanian–Maastrichtian), Red Deer River Valley, Alberta, Canada. – Canadian Journal of Earth Sciences, 57(10): 1220–1237.
<https://doi.org/10.1139/cjes-2019-0019>
- Edmonds, N. L., Stockey, R. A., Rothwell, G. W. (2022): Late Cretaceous aquatic vegetation: *Tolmania aquatica* gen. et sp. nov., from southern Alberta, Canada. – International Journal of Plant Sciences, 183: 567–575.
<https://doi.org/10.1086/721261>
- Eckenwalder, J. E. (2009): Conifers of the World. – Portland, OR: Timber Press.
- Ellis, B., Daly, D., Hickey, L., Johnson, K., Mitchell, J., Wilf, P., Wing, S. (2009): Manual of Leaf Architecture. – Ithaca, NY: Cornell University Press, 220 pp.
<https://doi.org/10.1079/9781845935849.0000>
- Elpe, C., Wang, X., Jin, J., Schneider, H. (2017): Cuticle micromorphology and the evolution of characters in the leaves of Taxaceae s.l. – Botanical Journal of the Linnean Society, 184: 503–517.
<https://doi.org/10.1093/botlinnean/box038>
- Escapa, I. H., Cúneo, R., Axsmith, B. (2008): A new genus of the Cupressaceae (*sensu lato*) from the Jurassic of Patagonia: implications for conifer megasporangiate cone homologies. – Review of Palaeobotany and Palynology, 151: 110–122.
<https://doi.org/10.1016/j.revpalbo.2008.03.002>
- Escapa, I. H., Herendeen, P. S., Rothwell, G. W., Stockey, R. A. (2016): A new species of *Athrotaxites* (Athrotaxoideae, Cupressaceae) from the Upper Cretaceous Raritan Formation, New Jersey, USA. – Botany, 94: 831–845.
<https://doi.org/10.1139/cjb-2016-0061>
- ESRI (2023): ArcGIS Pro: Release 3.1.0. Redlands, CA: Environmental Systems Research Institute.
- Evans, D. C., Eberth, D. A., Ryan, M. J. (2015): Hadrosaurid (*Edmontosaurus*) bonebeds from the Horseshoe Canyon Formation (Horseshoe member) at Drumheller, Alberta, Canada: geology, preliminary taphonomy, and significance. – Canadian Journal of Earth Sciences, 52(8): 642–654.
<https://doi.org/10.1139/cjes-2014-0184>
- Farjon, A. (2005): A Monograph of Cupressaceae and *Sciadopitys*. – Royal Botanic Gardens, Kew, 643 pp.
- Ferguson, D. K. (1967): On the phytogeography of Coniferales in the European Cenozoic. – Palaeogeography, Palaeoclimatology, Palaeoecology, 3: 73–110.
[https://doi.org/10.1016/0031-0182\(67\)90007-7](https://doi.org/10.1016/0031-0182(67)90007-7)
- 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>
- Flynn, A. G., Peppe, D. J. (2019): Early Paleocene tropical forest from the Ojo Alamo Sandstone, San Juan Basin,

- New Mexico, USA. – *Paleobiology*, 45(4): 612–635.
<https://doi.org/10.1017/pab.2019.24>
- Fontaine, W. M. (1889): The Potomac or Younger Mesozoic Flora. – U.S. Geological Survey, Monograph, 15: 377.
<https://doi.org/10.5962/bhl.title.36034>
- Friedrich, O., Herrle, J. O., Wilson, P. A., Cooper, M. J., Erbacher, J., Hemleben, C. (2009): Early Maastrichtian carbon cycle perturbation and cooling event: implications from the South Atlantic Ocean. – *Paleoceanography*, 24(2): PA2211 (14 pp.).
<https://doi.org/10.1029/2008PA001654>
- Gardner, J. S. (1887): On the Leaf-Beds and Gravels of Ardtun, Carsaig, etc. in Mull, with Notes by G. A. C. Cole. – *Quarterly Journal of the Geological Society*, 43(1-4): 270–300.
<https://doi.org/10.1144/GSL.JGS.1887.043.01-04.24>
- Golovneva, L. B. (2009): The morphology, taxonomy, and occurrence of the genus *Pseudoprotophyllum* Hollick (Platanaceae) in Late Cretaceous floras of Northern Asia. – *Palaeontological Journal*, 43(10): 1230–1244.
<https://doi.org/10.1134/S0031030109100050>
- Golovneva, L. B., Alekseev, P. I. (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>
- Graham, A. (1993): History of the vegetation: Cretaceous (Maastrichtian)–Tertiary. – *Flora of North America*, 1: 57–70.
- Greenwood, D. R., Conran, J. G., West, C. K. (2022): Palm fronds from western Canada are the northernmost palms from the Late Cretaceous of North America and may include the oldest Arecaceae. – *Review of Palaeobotany and Palynology*, 301: 104641 (20 pp.).
<https://doi.org/10.1016/j.revpalbo.2022.104641>
- Harris, T. M. (1979): The Yorkshire Jurassic Flora. V. Coniferales. – *British Museum (Natural History)*, 803: 1–166.
- Halbwidl, K., Seyfullah, L. J., West, C. K. (2026): Permineralised *Torreya* (Taxaceae) leaves from the Upper Cretaceous of Southern Alberta, Canada. – *Cretaceous Research*, 184: 106339 (19 pp.).
<https://doi.org/10.1016/j.cretres.2026.106339>
- Herendeen, P. S. (2017): Report of the Nomenclature Committee on Fossils: 11. – *Taxon*, 66(1): 193–196.
<https://doi.org/10.12705/661.17>
- Herendeen, P. S., Friis, E. M., Pedersen, K. R., Crane, P. R. (2017): Palaeobotanical redux: revisiting the age of the angiosperms. – *Nature Plants*, 3(3): 1–8.
<https://doi.org/10.1038/nplants.2017.15>
- Herman, A. B. (2002): Late Early–Late Cretaceous floras of the North Pacific Region: florogenesis and early angiosperm invasion. – *Review of Palaeobotany and Palynology*, 122(1-2): 1–11.
[https://doi.org/10.1016/S0034-6667\(02\)00085-4](https://doi.org/10.1016/S0034-6667(02)00085-4)
- Hickey, L. J. (2001): On the nomenclatural status of the morpho-genera, *Quereuxia* and *Trapago*. – *Taxon*, 50: 1119–1124.
<https://doi.org/10.2307/1224729>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., Jarvis, A. (2005): Very high resolution interpolated climate surfaces for global land areas. – *International Journal of Climatology*, 25(15): 1965–1978.
<https://doi.org/10.1002/joc.1276>
- Hollick, C. A. (1930): The Upper Cretaceous Floras of Alaska (No. 159). – US Government Printing Office, Washington, 123 pp., 68 pls.
- Huegele, I. B., Wang, H. (2023): An unusual plane tree from the Early Cretaceous of Kansas, USA. – *Review of Palaeobotany and Palynology*, 309: 104815 (15 pp.).
<https://doi.org/10.1016/j.revpalbo.2022.104815>
- IFPNI (2014–): The International Fossil Plant Names Index. Global registry of scientific names of fossil organisms covered by the International Code of Nomenclature for Algae, Fungi, and Plants and the International Code of Zoological Nomenclature. <http://ifpni.org/> [accessed 24. 6. 2025].
- Johnson, K. R. (1992): Leaf-fossil evidence for extensive floral extinction at the Cretaceous–Tertiary boundary, North Dakota, USA. – *Cretaceous Research*, 13: 91–117.
[https://doi.org/10.1016/0195-6671\(92\)90029-P](https://doi.org/10.1016/0195-6671(92)90029-P)
- Johnson, K. R. (1996): Description of Seven Common Fossil Leaf Species from the Hell Creek Formation (Upper Cretaceous: Upper Maastrichtian), North Dakota, South Dakota, and Montana. – *Denver Museum of Natural History*, Denver, 47 pp.
- Johnson, K. R. (2002): Megaflora of the Hell Creek and lower Fort Union formations in the western Dakotas: vegetational response to climate change, the Cretaceous–Tertiary boundary event, and rapid marine transgression. – In: Hartman, J., Johnson, K. R., Nichols, D. J. (eds), *The Hell Creek Formation and the Cretaceous–Tertiary Boundary in the Northern Great Plains*. Geological Society of America Special Paper, 361: 329–391.
<https://doi.org/10.1130/0-8137-2361-2.329>
- Jonsson, C. H., Hebda, R. J. (2015): Macroflora, paleogeography, and paleoecology of the Upper Cretaceous (Turonian?–Santonian) Saanich Member of the Comox Formation, Saanich Peninsula, British Columbia, Canada. – *Canadian Journal of Earth Sciences*, 52(7): 519–536.
<https://doi.org/10.1139/cjes-2014-0180>
- Johnson, K. R., Nichols, D. J., Attrep, M., Orth, C. J., Wiener, M. C. (1989): High-resolution leaf-fossil record spanning the Cretaceous/Tertiary boundary. – *Nature*, 340: 708–711.
<https://doi.org/10.1038/340708a0>
- Johnson, K. R., Reynolds, M. L., Werth, K. W., Thomasson, J. R. (2003): Overview of the Late Cretaceous, early Paleocene, and early Eocene megaflores of the Denver Basin, Colorado. – *Rocky Mountain Geology*, 38(1): 101–120.
<https://doi.org/10.2113/gsrocky.38.1.101>
- Kalyniuk, J. E., West, C. K., Greenwood, D. R., Basinger, J. F., Brown, C. M. (2023): The Albian vegetation of central Alberta as a food source for the nodosaurid *Borealopelta markmitchelli*. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 611: 111356 (16 pp.).
<https://doi.org/10.1016/j.palaeo.2022.111356>
- Kimura, T., Sekido, S. (1975): *Nilssoniocladus* n. gen. (Nilssoniaceae, n. fam.), newly found from the early Lower Cretaceous of Japan. – *Palaeontographica B*, 153(1-3): 111–118.

- Kirkpatrick, J. B., DellaSala, D. A. (2011): Temperate rainforests of Australasia. In: – DellaSala, D. A. (ed.), *Temperate and Boreal Rainforests of the World: Ecology and Conservation*. Island Press/Center for Resource Economics, Washington, D.C., pp. 195–212.
https://doi.org/10.5822/978-1-61091-008-8_8
- Klymiuk, A. A., Stockey, R. A., Rothwell, G. W. (2015): Plant–arthropod interactions in *Acanthostrobus edenensis* (Cupressaceae), a new conifer from the Upper Cretaceous of Vancouver Island, British Columbia. – *International Journal of Plant Sciences*, 176(4): 378–392.
<https://doi.org/10.1086/680684>
- Koppelhus, E. B. (2005): Paleobotany. – In: Koppelhus, E. B., Currie, P. J. (eds), *Dinosaur Provincial Park: A spectacular Ancient Ecosystem Revealed*. Indiana University Press, Bloomington, pp. 131–138.
- Lebourgeois, F., Pierrat, J. C., Perez, V., Piedallu, C., Cecchini, S., Ulrich, E. (2010): Simulating phenological shifts in French temperate forests under two climatic change scenarios and four driving global circulation models. – *International Journal of Biometeorology*, 54(5): 563–581.
<https://doi.org/10.1007/s00484-010-0305-5>
- LePage, B. A. (2011): A classification system to separate leaves of the Cephalotaxaceae, Taxaceae, and Taxodiaceae. – *Japanese Journal of Historical Botany*, 19(1-2): 109–116.
- Lesquereux, L. (1873): Lignitic Formation and fossil flora. – In Hayden, F. V. (ed.), *Sixth Annual Report of the United States Geological Survey of the Territories, Embracing Portions of Montana, Idaho, Wyoming, and Utah, Being a Report of Progress of the Explorations for the Year 1872*. Government Printing Office, Washington D.C., pp. 317–427.
- Lesquereux, L. (1878): Contributions to the Fossil Flora of the Western Territories, Vol. 7. – United States Geological Survey of the Territories, Washington, D.C., 366 pp.
- Loidi, J., Chytrý, M., Jiménez-Alfaro, B., Alessi, N., Biurrun, I., Campos, J. A., Čarni, A., Fernández-Pascual, E., Font Castell, X., Gholizadeh, H., Indreica, A., Kavgaci, A., Knollová, I., Naqinezhad, A., Novák, P., Nowak, A., Škvorc, Ž., Tsiripidis, I., Vassilev, K., Marcenó, C. (2020): Life-form diversity across temperate deciduous forests of Western Eurasia: a different story in the understory. – *Journal of Biogeography*, 48(11): 2932–2945.
<https://doi.org/10.1111/jbi.14254>
- 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: 433–448.
<https://doi.org/10.1016/j.palaeo.2018.09.010>
- Lupia, R., Crane, P. R., Lidgard, S. (2000): Angiosperm diversification and Cretaceous environmental change. – In: Culver, S. J., Rawson, P. F. (eds), *Biotic Responses to Global Change: The Last 145 Million Years*. Cambridge University Press, Cambridge, pp. 207–222.
<https://doi.org/10.1017/CBO9780511535505.016>
- Lupia, R., Lidgard, S., Crane, P. R. (1999): Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation. – *Paleobiology*, 25: 305–340.
<https://doi.org/10.1017/S009483730002131X>
- MacLeod, S. E., Hills, L. V. (1991): Late Jurassic to Early Cretaceous (Tithonian to pre-Albian) plant macrofossils, northern Bowser Basin, British Columbia, Canada. – *Review of Palaeobotany and Palynology*, 70(1-2): 9–45.
[https://doi.org/10.1016/0034-6667\(91\)90076-F](https://doi.org/10.1016/0034-6667(91)90076-F)
- Manchester, S. R. (1986): Vegetative and reproductive morphology of an extinct plane tree (Platanaceae) from the Eocene of western North America. – *Botanical Gazette*, 147(2): 200–226.
<https://doi.org/10.1086/337587>
- Manchester, S. R. (2014): Revisions to Roland Brown's North American Paleocene flora. – *Acta Musei Nationalis Pragae, Series B – Historia Naturalis*, 70: 153–210.
<https://doi.org/10.14446/AMNP.2014.153>
- Manchester, S. R., Chen, Z. D. (1998): A new genus of Coryloideae (Betulaceae) from the Paleocene of North America. – *International Journal of Plant Sciences*, 159(3): 522–532.
<https://doi.org/10.1086/297569>
- Manchester, S. R., Shuang-Xing, G. (1996): *Palaeocarpinus* (extinct Betulaceae) from northwestern China: new evidence for Paleocene floristic continuity between Asia, North America, and Europe. – *International Journal of Plant Sciences*, 157(2): 240–246.
<https://doi.org/10.1086/297343>
- Manchester, S. R., Pigg, K. B., Crane, P. R. (2004): *Palaeocarpinus dakotensis* sp. n. (Betulaceae: Coryloideae) and associated staminate catkins, pollen, and leaves from the Paleocene of North Dakota. – *International Journal of Plant Sciences*, 165(6): 1135–1148.
<https://doi.org/10.1086/423870>
- Maslova, N. P., Moiseeva, M. G., Herman, A. B., Kvaček, J. (2005): Did plane trees exist in the Cretaceous? – *Paleontological Journal*, 39(4): 440.
- McIver, E. E. (2002): The paleoenvironment of *Tyrannosaurus rex* from southwestern Saskatchewan, Canada. – *Canadian Journal of Earth Sciences*, 39(2): 207–221.
<https://doi.org/10.1139/e01-073>
- McIver, E. E., Aulenback, K. R. (1994): Morphology and relationships of *Mesocyparis umbonata* sp. nov.: fossil Cupressaceae from the Late Cretaceous of Alberta, Canada. – *Canadian Journal of Botany*, 72(3): 273–295.
<https://doi.org/10.1139/b94-037>
- 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. (1989): The morphology and relationships of *Equisetum fluviatoides* sp. nov. from the Paleocene Ravenscrag Formation of Saskatchewan, Canada. – *Canadian Journal of Botany*, 67(10): 2937–2943.
<https://doi.org/10.1139/b89-376>
- McIver, E. E., Basinger, J. F. (1993): Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. – *Palaeontographica Canadiana*, (10): 1–167.
- McLoughlin, S. (1996): Early Cretaceous macrofloras of Western Australia. – *Records of the Western Australian*

- Museum, 18: 19–66.
- Miller, I. M., Hickey, L. J. (2010): The fossil flora of the Winthrop Formation (Albian-Early Cretaceous) of Washington State, USA. Part II: Pinophytina. – *Bulletin of the Peabody Museum of Natural History*, 51(1): 3–96. <https://doi.org/10.3374/014.051.0104>
- Moiseeva, M. G. (2008): New angiosperms from the Maastrichtian of the Amaam Lagoon area (northeastern Russia). – *Paleontological Journal*, 42(3): 313–327. <https://doi.org/10.1134/S0031030108030131>
- Nayim, Y. S. (2017): Mapping of biotopes between Amasra and Inkum (Bartın), Western Black Sea Region of Turkey. – *Journal of Environmental Biology*, 38: 1033–1042. [https://doi.org/10.22438/jeb/38/5\(SI\)/GM-20](https://doi.org/10.22438/jeb/38/5(SI)/GM-20)
- Newberry, J. S. (1898): The later extinct floras of North America. – *United States Geological Survey Monograph*, 35: 1–295. <https://doi.org/10.5962/bhl.title.36429>
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., Borman, T. (2025): *vegan*: Community Ecology Package. R package version 2.6-10, <https://CRAN.R-project.org/package=vegan> [accessed 07.18. 2025].
- Pearson, J., Hebda, R. J. (2006): Paleoclimate of the Late Cretaceous Cranberry Arms flora of Vancouver Island: evidence for latitudinal displacement. In: Haggart, J., Enkin, R. J., Monger, J. W. H. (eds), *Paleogeography of the North American Cordillera: evidence for and against large-scale displacements*. Geological Association of Canada Special Paper, 46: 133–145.
- Peppe, D. J., Erickson, J. M., Hickey, L. J. (2007): Fossil leaf species from the Fox Hills Formation (Upper Cretaceous: North Dakota, USA) and their paleogeographic significance. – *Journal of Paleontology*, 81(3): 550–567. <https://doi.org/10.1666/05067.1>
- Pott, C., Kerp, H., Krings, M. (2007): Morphology and epidermal anatomy of *Nilssonia* (cycadalean foliage) from the Upper Triassic of Lunz (Lower Austria). – *Review of Palaeobotany and Palynology*, 143(3-4): 197–217. <https://doi.org/10.1016/j.revpalbo.2006.07.007>
- Quinney, A., Therrien, F., Zelenitsky, D. K., Eberth, D. A. (2013): Palaeoenvironmental and palaeoclimatic reconstruction of the Upper Cretaceous (late Campanian–early Maastrichtian) Horseshoe Canyon Formation, Alberta, Canada. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 371: 26–44. <https://doi.org/10.1016/j.palaeo.2012.12.009>
- R Core Team (2024): R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> [accessed 06.14. 2024].
- Reichgelt, T., West, C. K. (2025): Insights into greener Miocene biomes and globally enhanced terrestrial productivity from fossil leaves. – *Evolving Earth*, 3: 100058 (13 pp.). <https://doi.org/10.1016/j.eve.2025.100058>
- Rothwell, G. A., Basinger, J. F. (1979): *Metasequoia milleri* n. sp., anatomically preserved pollen cones from the Middle Eocene (Allenby Formation) of British Columbia. – *Canadian Journal of Botany*, 57: 958–970. <https://doi.org/10.1139/b79-118>
- Rothwell, G. W., Stockey, R. A. (2022): Enriching our knowledge of Late Cretaceous wetland plant communities: *Zlatkovia crenulata* gen. et sp. nov., an amphibious angiosperm from the St. Mary River Formation, Alberta, Canada. – *Cretaceous Research*, 140: 105328 (9 pp.). <https://doi.org/10.1016/j.cretres.2022.105328>
- Rothwell, G. W., Stockey, R. A., Smith, S. Y. (2020): Revisiting the Late Cretaceous *Parataxodium wigginsii* flora from the North Slope of Alaska, a high-latitude temperate forest. – *Cretaceous Research*, 116: 104592 (16 pp.). <https://doi.org/10.1016/j.cretres.2020.104592>
- Running, S. W., Mu, Q., Zhao, M. (2015): MOD17A3H MODIS/terra net primary production yearly L4 global 500m SIN grid V006. NASA EOSDIS Land Processes DAAC. <https://doi.org/10.5067/MODIS/MOD17A3H.006>
- Schneider, C. A., Rasband, W. S., Eliceiri, K. W. (2012): NIH Image to ImageJ: 25 years of image analysis. – *Nature Methods*, 9(7): 671–675. <https://doi.org/10.1038/nmeth.2089>
- Schweitzer, H.-J. (1974): Die tertiären Koniferen Spitzbergens. – *Palaeontographica B*, 149: 1–89.
- Serbet, R., Bomfleur, B., Rothwell, G. W. (2013): *Cunninghamia taylorii* sp. nov., a structurally preserved cupressaceous conifer from the Upper Cretaceous (Campanian) Horseshoe Canyon Formation of western North America. – *International Journal of Plant Sciences*, 174: 471–488. <https://doi.org/10.1086/668695>
- Serbet, R., Rothwell, G. W. (1999): *Osmunda cinnamomea* (Osmundaceae) in the Upper Cretaceous of western North America: additional evidence for exceptional species longevity among filicalean ferns. – *International Journal of Plant Sciences*, 160: 425–433. <https://doi.org/10.1086/314134>
- Serbet, R., Rothwell, G. W. (2003): Anatomically preserved ferns from the Late Cretaceous of western North America: Dennstaedtiaceae. – *International Journal of Plant Sciences*, 164: 1041–1051. <https://doi.org/10.1086/378652>
- Serbet, R., Rothwell, G. W. (2006): Anatomically preserved ferns from the Late Cretaceous of western North America. II. Blechnaceae/Dryopteridaceae. – *International Journal of Plant Sciences*, 167: 703–709. <https://doi.org/10.1086/500996>
- Serbet, R., Rothwell, G. W. (2025): *Drumhelleria kurmanniae* Serbet and Stockey; reconstructing a sequoioid conifer (Cupressaceae) from the Late Cretaceous (Campanian–Maastrichtian) of Western Canada. – *International Journal of Plant Sciences*, 186: 193–214. <https://doi.org/10.1086/734305>
- Serbet, R., Stockey, R. A. (1991): Taxodiaceous pollen cones from the Upper Cretaceous (Horseshoe Canyon Formation) of Drumheller, Alberta, Canada. – *Review of Palaeobotany and Palynology*, 70: 67–76.

- [https://doi.org/10.1016/0034-6667\(91\)90078-H](https://doi.org/10.1016/0034-6667(91)90078-H)
- Seward, A. C. (1919): Fossil Plants, Vol. IV: Ginkgoales, Coniferales, Gnetales. – Cambridge University Press, Cambridge, 543 pp.
- Spicer, R. A. (1989): Plants at the Cretaceous-Tertiary boundary. – Philosophical Transactions of the Royal Society of London B, 325(1228): 291–305.
<https://doi.org/10.1098/rstb.1989.0090>
- Spicer, R. A. (2008): Frontiers in palaeobotany: plant fossils and their role in predicting future climate change. – Journal of Palaeosciences, 57(1-3): 415–427.
<https://doi.org/10.54991/jop.2008.257>
- Spicer, R. A., Herman, A. B. (1996): *Nilssoniocladus* in the Cretaceous Arctic: new species and biological insights. – Review of Palaeobotany and Palynology, 92(3-4): 229–243.
[https://doi.org/10.1016/0034-6667\(95\)00111-5](https://doi.org/10.1016/0034-6667(95)00111-5)
- Spicer, R. A., Herman, A. B. (2010): The Late Cretaceous environment of the Arctic: a quantitative reassessment based on plant fossils. – Palaeogeography, Palaeoclimatology, Palaeoecology, 295(3-4): 423–442.
<https://doi.org/10.1016/j.palaeo.2010.02.025>
- Spicer, R. A., Parrish, J. T., Grant, P. R. (1992): Evolution of vegetation and coal-forming environments in the Late Cretaceous of the North Slope of Alaska. – In: McCabe, P. J., Parrish, J. T. (eds), Controls on the Distribution and Quality of Cretaceous Coals. Geological Society of America, Special Paper, 267: 177–192.
<https://doi.org/10.1130/SPE267-p177>
- Spicer, R. A., Yang, J., Spicer, T. E., Farnsworth, A. (2021): Woody dicot leaf traits as a palaeoclimate proxy: 100 years of development and application. – Palaeogeography, Palaeoclimatology, Palaeoecology, 562: 110138 (20 pp.).
<https://doi.org/10.1016/j.palaeo.2020.110138>
- Stanich, N. A., Rothwell, G. W., Stockey, R. A. (2009): Phylogenetic diversification of *Equisetum* (Equisetales) as inferred from Lower Cretaceous species of British Columbia, Canada. – American Journal of Botany, 96(7): 1289–1299.
<https://doi.org/10.3732/ajb.0800381>
- Ștefan, V., Levin, S. (2018): plotbiomes: R package for plotting Whittaker biomes with ggplot2 (v1.0.0). Zenodo. [accessed 08.04.2025].
<https://doi.org/10.5281/zenodo.7145245>
- Stockey, R. A. (1982): The Araucariaceae: an evolutionary perspective. – Review of Palaeobotany and Palynology, 37(1-2): 133–154.
[https://doi.org/10.1016/0034-6667\(82\)90041-0](https://doi.org/10.1016/0034-6667(82)90041-0)
- Stockey, R. A., Rothwell, G. W. (1997): The aquatic angiosperm *Trapago angulata* from the Upper Cretaceous (Maastrichtian) St. Mary River Formation of southern Alberta. – International Journal of Plant Sciences, 158(1): 83–94.
<https://doi.org/10.1086/297417>
- Stockey, R. A., Rothwell, G. A., Atkinson, B. A. (2020): Late Cretaceous diversification of cupressaceous conifers: a taiwanioid seed cone from the Eden Main, Vancouver Island, British Columbia, Canada. – International Journal of Plant Sciences, 181(5): 529–541.
<https://doi.org/10.1086/708383>
- Stockey, R. A., Rothwell, G. W., Falder, A. B. (2001): Diversity among taxodioid conifers: *Metasequoia foxii* sp. nov. from the Paleocene of central Alberta, Canada. – International Journal of Plant Sciences, 162: 221–234.
<https://doi.org/10.1086/317914>
- Thibault, N., Harlou, R., Schovsbo, N. H., Stemmerik, L., Surlyk, F. (2016): Late Cretaceous (late Campanian–Maastrichtian) sea-surface temperature record of the Boreal Chalk Sea. – Climate of the Past, 12(2): 429–438.
<https://doi.org/10.5194/cp-12-429-2016>
- Tralau, H. (1968): Evolutionary trends in the genus *Ginkgo*. – Lethaia, 1(1): 63–101.
<https://doi.org/10.1111/j.1502-3931.1968.tb01728.x>
- Ward, L. F. (1886): Synopsis of the flora of the Laramie Group. – In: Sixth Annual Report of the United States Geological Survey, 1884–1885. Government Printing Office, Washington, DC, pp. 399–570.
<https://doi.org/10.5962/bhl.title.7835>
- Watson, J., Batten, D. J. (1990): A revision of the English Wealden flora, II. Equisetales. – Bulletin of the British Museum (Natural History) Geology, 46: 37–60.
- Watson, J., Lydon, S. J., Harrison, N. A. (1999): Consideration of the genus *Ginkgoites* Seward and a redescription of two species from the Lower Cretaceous of Germany. – Cretaceous Research, 20(6): 719–734.
<https://doi.org/10.1006/cres.1999.0178>
- West, C. K., Greenwood, D. R., Basinger, J. F. (2019): The late Paleocene to early Eocene Arctic megaflora of Ellesmere and Axel Heiberg islands, Nunavut, Canada; The late Paleocene to early Eocene Arctic megaflora of Ellesmere and Axel Heiberg islands, Nunavut, Canada. – Palaeontographica B, 300(1-6): 47–163.
<https://doi.org/10.1127/palb/2019/0066>
- West, C. K., Greenwood, D. R., Reichgelt, T., Lowe, A. J., Vachon, J. M., Basinger, J. F. (2020): Paleobotanical proxies for early Eocene climates and ecosystems in northern North America from middle to high latitudes. – Climate of the Past, 16(4): 1387–1410.
<https://doi.org/10.5194/cp-16-1387-2020>
- West, C. K., Reichgelt, T., Basinger, J. F. (2021): The Ravenscrag Butte flora: Paleoclimate and paleoecology of an early Paleocene (Danian) warm-temperate deciduous forest near the vanishing inland Cannonball Seaway. – Palaeogeography, Palaeoclimatology, Palaeoecology, 576: 110488 (14 pp.).
<https://doi.org/10.1016/j.palaeo.2021.110488>
- West, C. K., Reichgelt, T., Reyes, A. V., Buryak, S. D., Staniszewska, K. J., Basinger, J. F. (2024): Paleobotanical evidence for Mediterranean climates in the western Canadian paleoarctic during the late middle Eocene. – Paleogeography and Paleoclimatology, 39(10): e2024PA004874 (25 pp.).
<https://doi.org/10.1029/2024PA004874>
- Whittaker, R. H. (1962): Classification of natural communities. – The Botanical Review, 28: 1–239.
<https://doi.org/10.1007/BF02860872>
- Whittaker, R. H. (1975): Communities and Ecosystems, 2nd ed. – MacMillan Publishing, New York, 385 pp.
- Wilf, P. (1997): When are leaves good thermometers? A new case for leaf margin analysis. – Paleobiology, 23(3): 373–390.
<https://doi.org/10.1017/S0094837300019746>
- Wilf, P., Carvalho, M. R., Stiles, E. (2023): The end-Cretaceous plant extinction: heterogeneity, ecosystem

- transformation, and insights for the future. – Cambridge Prisms: Extinction, 1: e14 (10 pp.).
<https://doi.org/10.1017/ext.2023.13>
- Wilf, P., Johnson, K. R. (2004): Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafloral record. – *Paleobiology*, 30: 347–368.
[https://doi.org/10.1666/0094-8373\(2004\)030<0347:LPEATE>2.0.CO;2](https://doi.org/10.1666/0094-8373(2004)030<0347:LPEATE>2.0.CO;2)
- Wilf, P., Johnson, K. R., Huber, B. T. (2003): Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous–Paleogene boundary. – *Proceedings of the National Academy of Sciences*, 100(2): 599–604.
<https://doi.org/10.1073/pnas.0234701100>
- Wilf, P., Wing, S. L., Greenwood, D. R., Greenwood, C. L. (1998): Using fossil leaves as paleoprecipitation indicators: an Eocene example. – *Geology*, 26(3): 203–206.
[https://doi.org/10.1130/0091-7613\(1998\)026<0203:U-FLAPI>2.3.CO;2](https://doi.org/10.1130/0091-7613(1998)026<0203:U-FLAPI>2.3.CO;2)
- 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 B*, 341(1297): 243–252.
<https://doi.org/10.1098/rstb.1993.0109>
- Wolfe, J. A. (1975): Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. – *Annals of the Missouri Botanical Garden*, 62: 264–279.
<https://doi.org/10.2307/2395198>
- Wolfe, J. A. (1993): A Method of Obtaining Climatic Parameters from Leaf Assemblages (No. 2040–2041). – US Government Printing Office, Washington, D.C., 71 pp.
- Wolfe, J. A., Upchurch, G. R. Jr. (1986): Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary. – *Nature*, 324(6093): 148–152.
<https://doi.org/10.1038/324148a0>
- Wolfe, J. A., Upchurch, G. R. Jr. (1987): Leaf assemblages across the Cretaceous–Tertiary boundary in the Raton Basin, New Mexico and Colorado. – *Proceedings of the National Academy of Sciences*, 84(15): 5096–5100.
<https://doi.org/10.1073/pnas.84.15.5096>
- Yang, J., Spicer, R. A., Spicer, T. E., Arens, N. C., Jacques, F. M., Su, T., Kennedy, E. M., Herman, A. B., Steart, D. C., Srivastava, G., Mehrotra, R. C. (2015): Leaf form–climate relationships on the global stage: an ensemble of characters. – *Global Ecology and Biogeography*, 24(10): 1113–1125.
<https://doi.org/10.1111/geb.12334>
- Yang, J., Spicer, R. A., Spicer, T. E., Li, C. S. (2011): ‘CLAMP Online’: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. – *Palaeobiodiversity and Palaeoenvironments*, 91: 163–183.
<https://doi.org/10.1007/s12549-011-0056-2>
- Zolina, A., Golovneva, L. (2023): Type material of *Trochodendroides richardsonii* (Heer) Krysht. (Cercidiphyllaceae) from the Atanikerdluk (Paleocene, Greenland). – *Biological Communications*, 68(4): 297–306.
<https://doi.org/10.21638/spbu03.2023.409>
- Zolina, A. A., Manchester, S. R., Golovneva, L. B. (2021). Typification of the genus *Zizyphoides* Seward et Conway (Magnoliophyta, Trochodendraceae). – *Acta Palaeobotanica*, 61(2): 123–135.
<https://doi.org/10.35535/acpa-2021-0007>

Table 1. List of floral elements described from the Morrin Bridge macroflora assemblage. * = reported from Maastrichtian of Western Canada previously.

Monilophyta	
Equisetaceae	
<i>Equisetum</i> L. rhizome*	
Polypodiopsida	
Unidentified fern fragment	
Gymnosperms	
‘Cycadophyta’	
Unidentified cycadophyte 1	
Unidentified cycadophyte 2	
Nilssoniaceae	
<i>Nilssonia serotina</i> HEER*	
Ginkgopsida	
Ginkgoaceae	
<i>Ginkgoites</i> SEWARD sp. *	
<i>Ginkgoites pluripartitus</i> (SCHIMP.) SEWARD	
<i>Baiera</i> BRAUN	
Pinopsida	
Cupressaceae	
<i>Taxodium</i> RICH.*	
<i>Cupressinocladus interruptus</i> (NEWB.) KRASSILOV	
<i>Cupressinocladus</i> SEWARD sp. 1	
<i>Cupressinocladus</i> sp. 2	
<i>Elatocladus</i> sp. HALLE	
unidentified Sequoioideae ovuliferous cone 1	
unidentified Sequoioideae ovuliferous cone 2	
unidentified Cupressaceae ovuliferous cone	
unidentified Sequoioideae pollen cones	
Taxaceae	
<i>Torreyites</i> SEWARD *	
Incertae sedis	
<i>Conago</i> I.M.MILLER et HICKEY sp. 1	
<i>Conago</i> sp. 2	
<i>Pagiophyllum</i> HEER sp. 1	
<i>Pagiophyllum</i> sp. 2	
<i>Pagiophyllum</i> sp. 3	
Unidentified shoot fragment with falcate leaves	
Angiosperms	
Monocots	
Incertae sedis	
<i>Monocotylophyllum</i> E.REID et M.CHANDLER. sp. 1	
<i>Monocotylophyllum</i> sp. 2	
Dicots	
Platanaceae	
<i>Platanites</i> cf. <i>P. marginatus</i> (LESQ.) K.R.JOHNSON	
cf. <i>Pseudoprotophyllum</i> (HOLLICK) GOLOVNEVA	
<i>Platanophyllum</i> FONTAINE	
cf. <i>Platananthus</i> MANCHESTER	
Betulaceae	
<i>Corylites</i> J.S.GARDNER ex SEWARD et HOLTUM	
Cercidiphyllaceae	
<i>Trochodendroides arctica</i> (HEER) E.W.BERRY*	
<i>Archeampelos</i> McIVER et BASINGER	

Jenkinsella arctica (HEER) W.A.BELL*
Trochodendraceae
Zizyphoides flabella (NEWB.) P.R.CRANE,
MANCHESTER, et DILCHER
Incertae sedis
Dicotylophyllum SAPORTA ex WARD sp. 1
Dicotylophyllum sp. 2
Dicotylophyllum sp. 3
Dicotylophyllum sp. 4
Dicotylophyllum sp. 5
Dicotylophyllum sp. 6
Dicotylophyllum sp. 7
Dicotylophyllum sp. 8
Dicotylophyllum sp. 9

Dicotylophyllum sp. 10
Dicotylophyllum sp. 11
Dicotylophyllum sp. 12
Dicotylophyllum sp. 13
Dicotylophyllum sp. 14
Dicotylophyllum sp. 15
Dicotylophyllum sp. 16
Dicotylophyllum sp. 17
Carpolithes BRONGN. sp. 1
Carpolithes sp. 2
Carpolithes sp. 3
Carpolithes sp. 4
Unidentified seed cluster
Unidentified floral structure

Table 2. Comparisons of climate estimates based on leaf physiognomy of the Morrin Bridge macroflora from the lower Maastrichtian Horsethief Member of Alberta (this study) and macrofloras from the upper Maastrichtian Frenchman Formation of Saskatchewan (Bamforth et al. 2014; Text-fig. 1). Bamforth et al. (2014) used two different calibrations in CLAMP using CCA; however, we have summarized their estimates based on rounding up to whole numbers their minimum and maximum estimates expressed as a range with error ($\pm$) presented as the higher of any uncertainty value they provided. Bamforth et al. (2014) estimated coldest month (CMMT) and warmest month (WMMT) temperature values, whereas our estimates are quarterly (three consecutive months), but are comparable within the given uncertainties. Our WMP and DMP are monthly values whereas their Three Wet and Three Dry are precipitation amounts for three consecutive months; both are given in this table as cm.

Locality	MAT (°C)	WMMT/WQT (°C)	CMMT/CQT (°C)	Three Wet/WMP (cm)	Three Dry/DMP (cm)	RH (%)
Chambery Coulee	12–20 $\pm$ 3	21–22 $\pm$ 3	5–7 $\pm$ 3	62–66 $\pm$ 23 ($\div$ 3 = 21–22)	14–21 $\pm$ 14 ($\div$ 3 = 5–7)	61–64 $\pm$ 11
Grasslands National Park	14–16 $\pm$ 2	23–24 $\pm$ 3	7–9 $\pm$ 3	63–67 $\pm$ 23 ($\div$ 3 = 21–22)	16–24 $\pm$ 11 ($\div$ 3 = 5–8)	67–70 $\pm$ 11
Morrin Bridge	12.2 $\pm$ 2.1	20.0 $\pm$ 2.5	3.8 $\pm$ 3.2	15.5 $\pm$ 5.7/9.0 ($\times$ 3 = 46.5)	7.1 $\pm$ 3.9/9.0 ($\times$ 3 = 21.3)	81.8 $\pm$ 9.3

Explanations of the plates

PLATE 1

- Equisetum* root and tuber. TMP2025.019.0002. Scale 1 cm.
- Unidentified fern frond fragment. TMP2018.006.0235. Scale 1 cm.
- Unidentified cycadophyte 1 frond fragment. TMP1997.076.0213. Scale 1 cm.
- Unidentified cycadophyte 1 frond fragment with acute apex. TMP1997.076.0087. Scale 1 cm.
- Unidentified cycadophyte 2 frond fragment. TMP1997.076.0087. Scale 1 cm.
- Nilssonina serotina*. TMP1997.076.0426. Scale 1 cm.
- Ginkgoites pluipartitus* TMP2025.019.0004. Scale 1 cm.
- Ginkgoites* sp. TMP1997.076.0345. Scale 1 cm.
- Baiera* sp. TMP1997.076.0498. Scale 1 cm.
- Taxodium* pollen cones. TMP1997.076.0004. Scale 1 cm.
- Taxodium* pollen cones in a panicle. TMP2005.068.0017. Scale 1 cm.
- Leafy branchlets of *Cupressinocladus interruptus*. TMP2018.006.0239. Scale 1 cm.
- Leafy branch, *Cupressinocladus* sp. 1. TMP1997.076.0204. Scale 1 cm.

- Leafy branch with scale-like leaves, *Cupressinocladus* sp. 2. TMP1997.076.0420. Scale 1 cm.

PLATE 2

- Leafy branchlets of *Elatocladus* var. A. TMP1997.076.0414. Scale 1 cm.
- Leafy branchlets of *Elatocladus* var. B. TMP1997.076.0202. Scale 1 cm.
- Leafy branchlets of *Elatocladus* var. C. TMP1997.076.0088. Scale 1 cm.
- Leafy branchlets of *Elatocladus* var. D. TMP1997.076.0158. Scale 1 cm.
- Unidentified Sequoioideae ovuliferous cone 1. TMP2005.068.0028. Scale 1 cm.
- Unidentified Sequoioideae ovuliferous cone 2. TMP1997.076.0272. Scale 1 cm.
- Unidentified Cupressaceae ovuliferous cone. TMP1997.076.0119. Scale 1 cm.
- Unidentified Sequoioideae pollen cones. TMP1997.076.0240. Scale 1 cm.
- Unidentified Sequoioideae pollen cones. TMP1997.076.0114. Scale 1 cm.

10. Leafy branch of *Torreyites*. TMP2025.019.0010. Scale 1 cm.
11. Close up of leaves of *Torreyites*. TMP2025.019.0010. Scale 1 mm.
12. Coniferous ovuliferous cone of *Conago* sp. 1. TMP1997.076.0086. Scale 1 cm.

PLATE 3

1. *Conago* sp. 2. TMP1997.076.0105. Scale 1 cm.
2. Leafy branch of *Pagiophyllum* sp. 1. TMP2005.068.0082. Scale 1 cm.
3. Leafy branch of *Pagiophyllum* sp. 2. TMP2005.068.0090. Scale 1 cm.
4. Leafy branch of *Pagiophyllum* sp. 3. TMP1997.076.0417. Scale 1 cm.
5. Basal fragment of a leafy shoot with imbricated leaves. TMP1997.076.0415. Scale 1 cm.
6. Linear leaf fragment *Monocotylophyllum* sp. 1. TMP2018.006.0232. Scale 1 cm.
7. Leaf fragment of *Monocotylophyllum* sp. 2. TMP1997.076.0081. Scale 1 cm.
8. *Platanites* cf. *P. marginatus*. TMP1997.076.0150. Scale 1 cm.
9. *Platanites* cf. *P. marginatus*. TMP1997.076.0391. Scale 1 cm.

PLATE 4

1. *Pseudoprotophyllum* sp. TMP1997.076.0079. Scale 1 cm.
2. *Pseudoprotophyllum* sp. TMP1997.076.0077. Scale 1 cm.
3. *Platanophyllum* sp. TMP2025.019.0006. Scale 1 cm.
4. Infructescence cf. *Platananthus*. TMP1997.076.0125. Scale 1 cm.
5. *Jenkinsella arctica*. TMP1997.076.0437. Scale 1 cm.
6. *Corylites* sp. TMP1997.076.0037. Scale 1 cm.
7. *Trochodendroides arctica*. TMP1997.076.0497. Scale 1 cm.
8. *Trochodendroides arctica*. TMP1997.076.0424. Scale 1 cm.
9. *Trochodendroides arctica*. TMP1997.076.0327. Scale 1 cm.

PLATE 5

1. *Archeampelos* sp. TMP2025.019.0008. Scale 1 cm.
2. *Zizyphoides flabella*. TMP.1997.076.0182. Scale 1 cm.
3. *Dicotylophyllum* sp. 1. TMP1997.076.0183. Scale 1 cm.
4. Counterpart leaf base of *Archeampelos* sp. TMP2025.019.0008. Scale 1 cm.
5. *Dicotylophyllum* sp. 2. TMP1997.076.0435. Scale 1 cm.
6. *Dicotylophyllum* sp. 3. TMP1997.076.0315. Scale 1 cm.

7. *Dicotylophyllum* sp. 3. TMP1997.076.0026. Scale 1 cm.
8. *Dicotylophyllum* sp. 4. TMP1997.076.0282. Scale 1 cm.

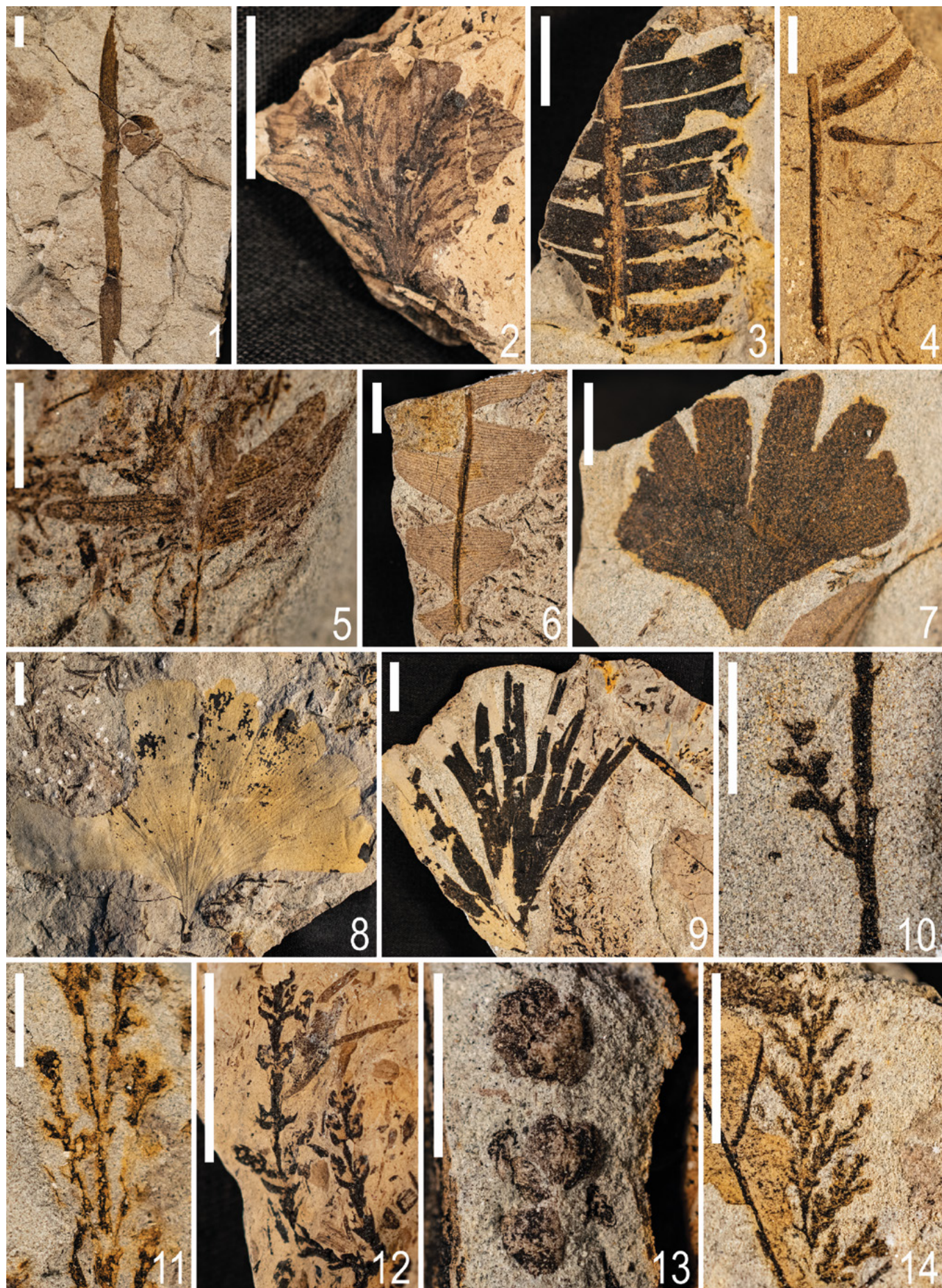
PLATE 6

1. *Dicotylophyllum* sp. 5. TMP2025.019.0003. Scale 1 cm.
2. *Dicotylophyllum* sp. 6. TMP1997.076.0368. Scale 1 cm.
3. *Dicotylophyllum* sp. 7. TMP1997.076.0374. Scale 1 cm.
4. *Dicotylophyllum* sp. 8. TMP2005.068.0092. Scale 1 cm.
5. *Dicotylophyllum* sp. 9. TMP2025.019.0009. Scale 1 cm.
6. *Dicotylophyllum* sp. 10. TMP2005.068.0092. Scale 1 cm.
7. *Dicotylophyllum* sp. 7. TMP1997.076.0311. Scale 1 cm.
8. *Dicotylophyllum* sp. 11. TMP1997.076.0272. Scale 1 cm.
9. *Dicotylophyllum* sp. 12. TMP2005.068.0044. Scale 1 cm.

PLATE 7

1. *Dicotylophyllum* sp. 13. TMP2025.019.0005. Scale 1 cm.
2. *Dicotylophyllum* sp. 14. TMP1997.076.0158. Scale 1 cm.
3. *Dicotylophyllum* sp. 15. TMP2025.019.0007. Scale 1 cm.
4. *Dicotylophyllum* sp. 16. TMP2025.019.0001. Scale 1 cm.
5. *Dicotylophyllum* sp. 17. TMP1997.076.0135. Scale 1 cm.
6. *Carpolithes* sp. 1. TMP1997.076.0198. Scale 1 cm.
7. *Carpolithes* sp. 2. TMP1997.076.0021. Scale 1 cm.
8. *Carpolithes* sp. 3. TMP1997.076.0222. Scale 1 cm.
9. *Carpolithes* sp. 4. TMP2018.006.0229. Scale 1 cm.
10. Unidentified seeds. TMP1997.076.0151. Scale 1 cm.
11. Unidentified floral structure. TMP1997.076.0001. Scale 1 cm.

PLATE 1



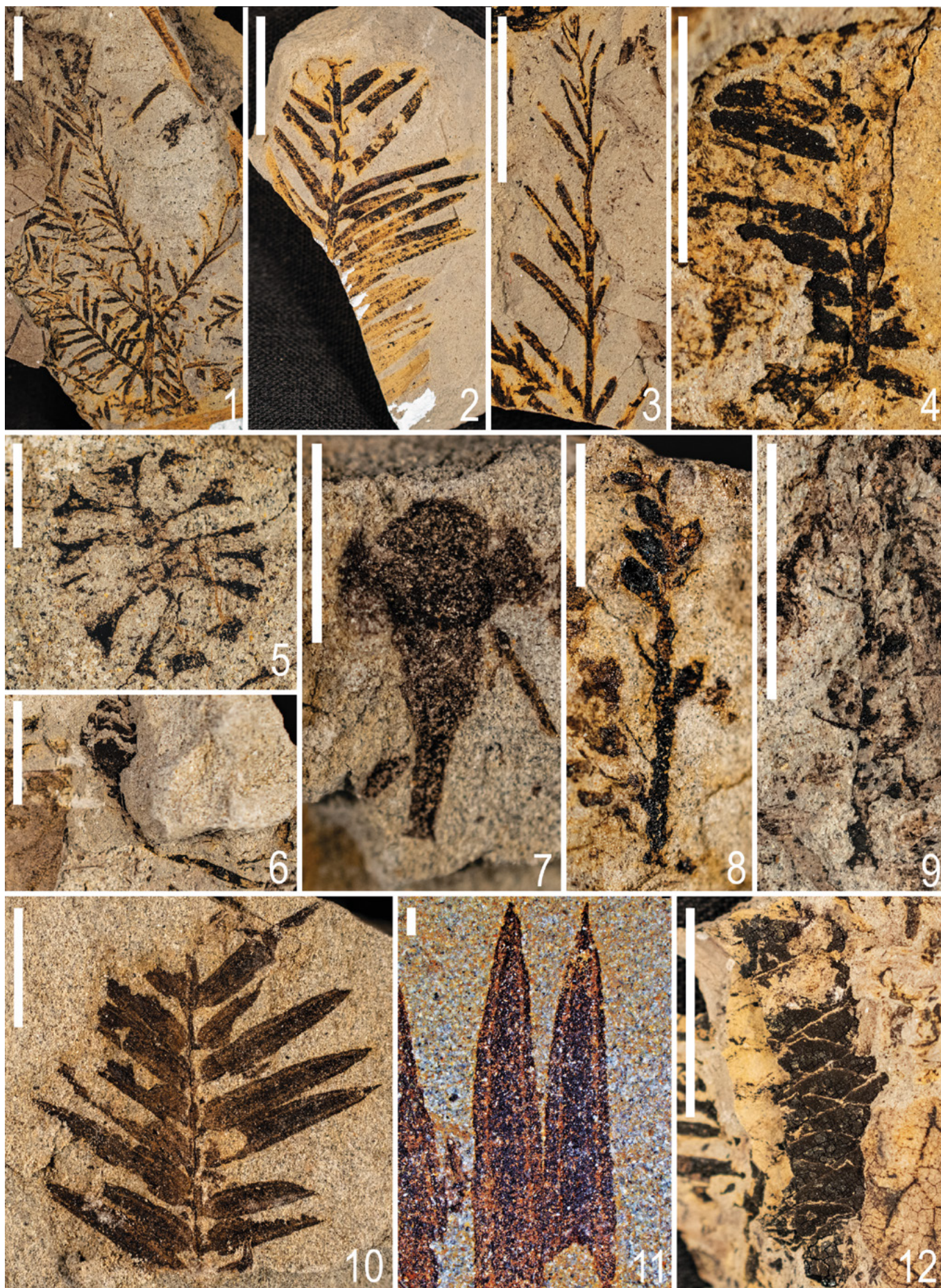
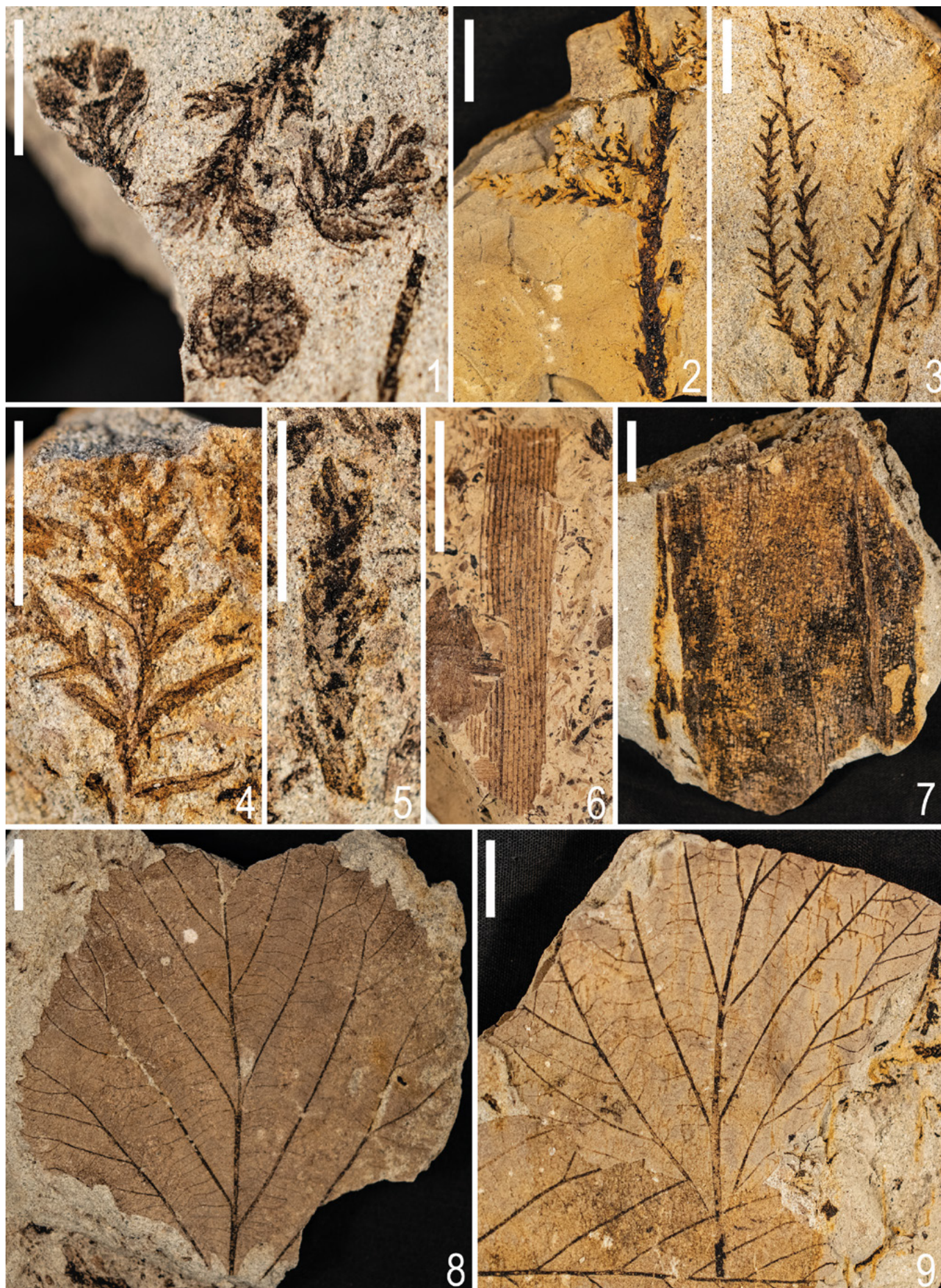
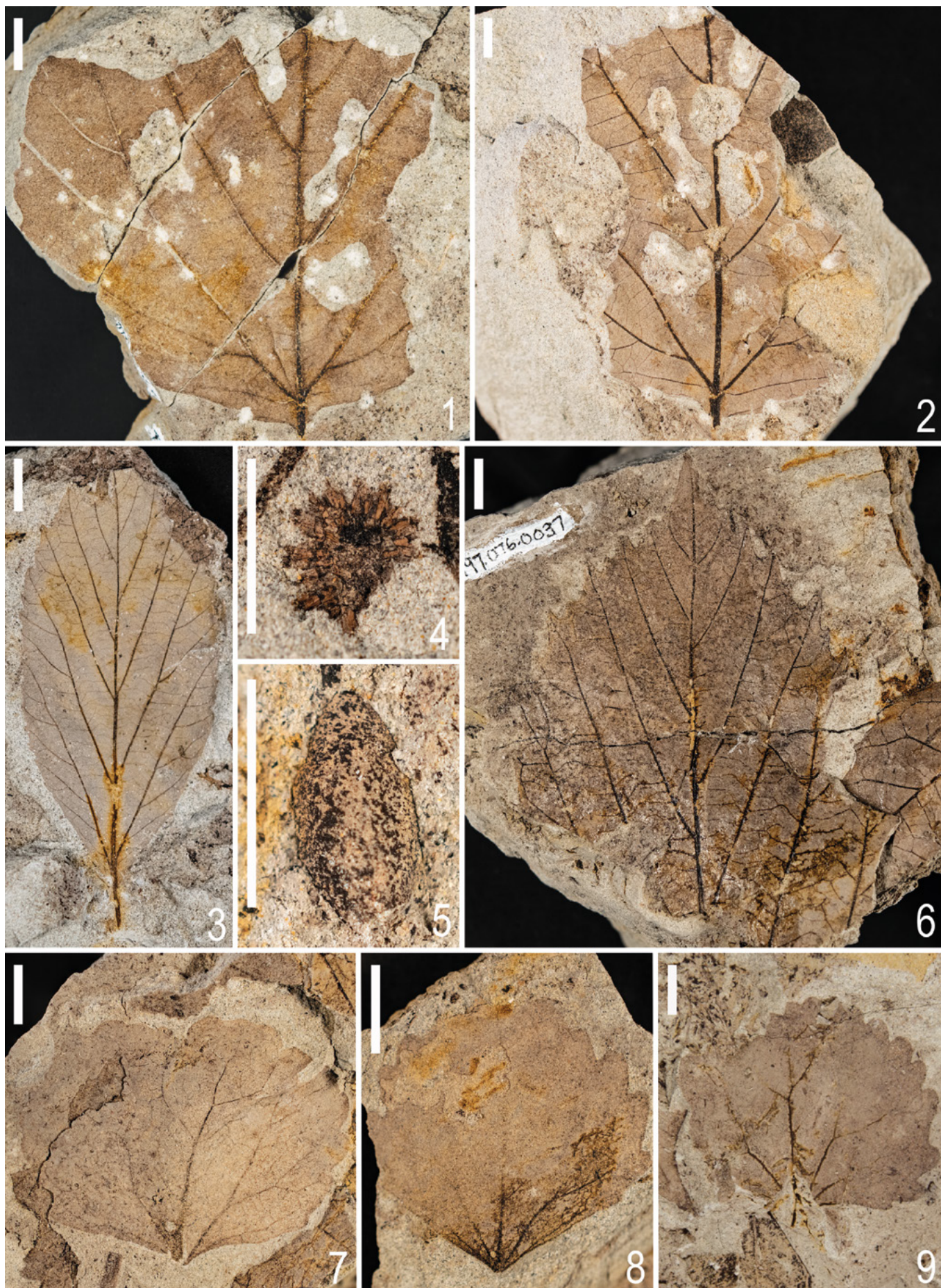
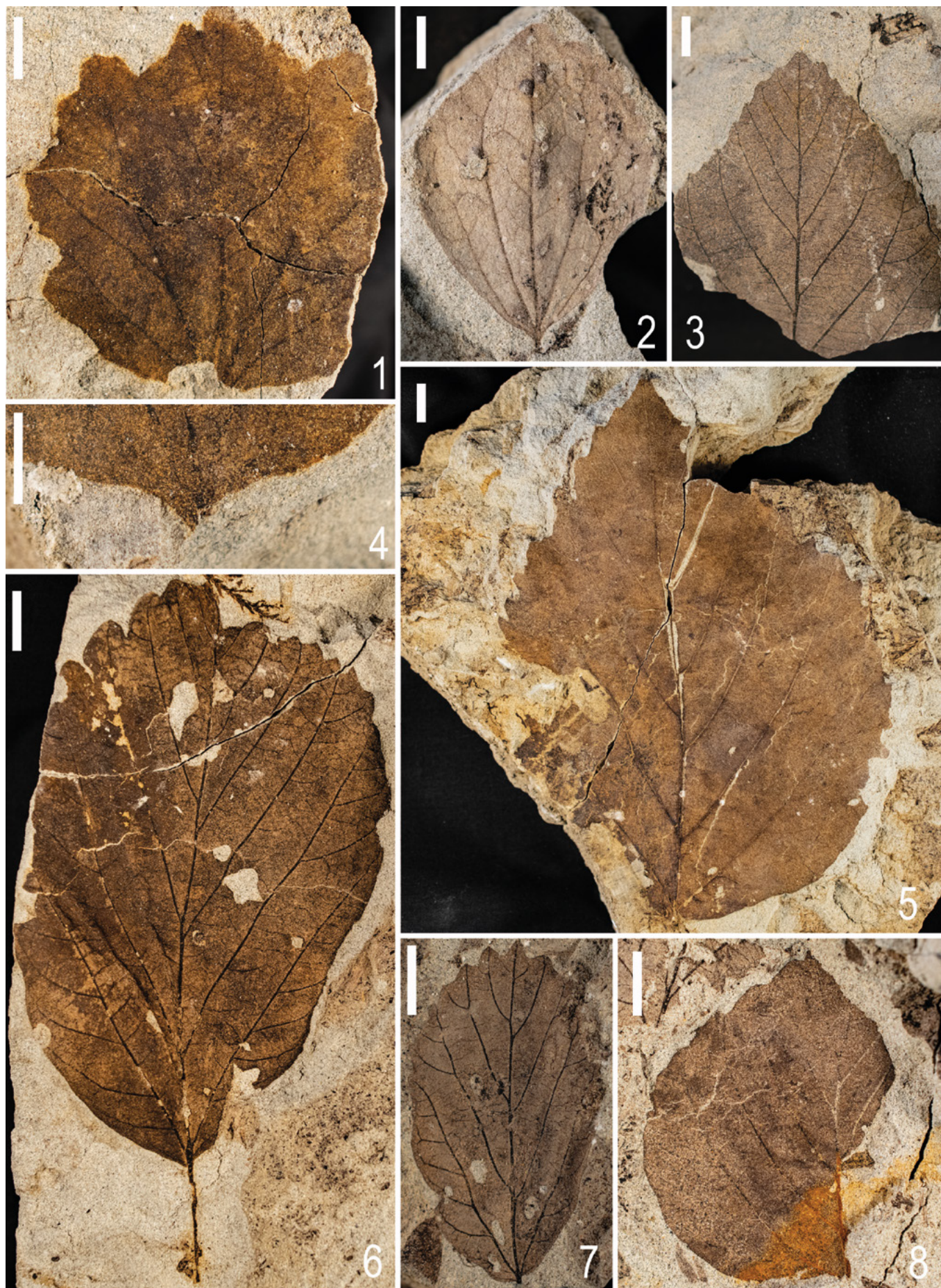


PLATE 3







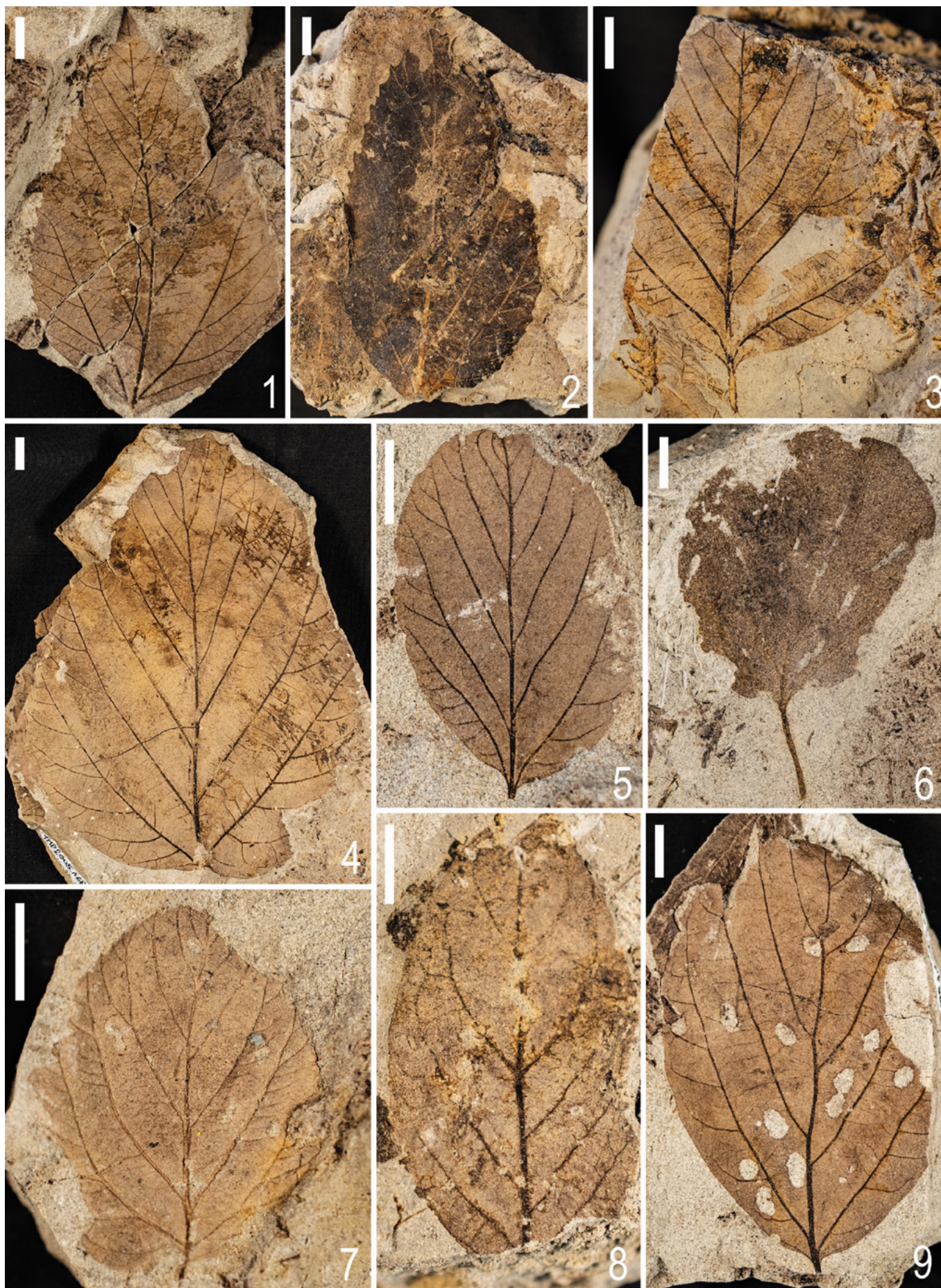


PLATE 7

