PUTATIVE *CELTIS* LEAVES FROM EOCENE PATAGONIA ARE ALLIED WITH ASIAN ANACARDIACEAE

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Short description: Abundant Eocene "*Celtis*" leaves from Laguna del Hunco in Patagonia are related to *Dobinea*, a mainland Asian genus of Anacardiaceae.

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Abstract. The most common macrofossils in the highly diverse flora from Laguna del Hunco (early Eocene of Chubut, Argentina) are "*Celtis*" *ameghinoi* leaves, whose true affinities have remained enigmatic for a century. The species accounts for 14% of all plant fossils in unbiased field counts and bears diverse insect-feeding damage, suggesting its high biomass and paleoecological importance. The leaves have well-preserved architecture but lack cuticles or reproductive attachments. We find that the fossils only superficially resemble *Celtis* and comparable taxa in Cannabaceae, Ulmaceae, Rhamnaceae, Malvaceae, and many other families. However, the distinctive foliar morphology conforms in detail to *Dobinea* (Anacardiaceae), a genus with two species of shrubs and large herbs ranging from India's Far East and Tibet to Myanmar and central China, and we propose *Dobineaites ameghinoi* (E.W. Berry) gen et. comb. nov. for the fossils. This discovery strengthens the extensive biogeographic links between Eocene Patagonia and mainland Asia, provides the first fossil record related to *Dobinea*, and represents a rare Gondwanan macrofossil occurrence of Anacardiaceae, which was widespread and diversified in the Northern Hemisphere at the time. The diverse leaf architecture of Anacardiaceae includes several patterns usually associated with other taxa, and many other leaf fossils in this family may remain misidentified.

Key words. Anacardiaceae. Argentina. Chinese flora. *Dobinea*. Gondwana. Herbivory. Laguna del Hunco. Leaf architecture.

Resumen. HOJAS DE "*CELTIS*" DEL EOCENO DE PATAGONIA VINCULADAS CON ANACARDIACEAE ASIÁTICAS. Los macrofósiles más comunes en la flora altamente diversa de la Laguna del Hunco (Eoceno temprano de Chubut, Argentina) son hojas de "*Celtis*" *ameghinoi*, conocidas desde hace un siglo y cuyas afinidades han sido enigmáticas. La especie representa el 14% del total de las hojas fósiles en censos imparciales de campo, y los ejemplares exhiben diversos daños producidos por alimentación de insectos, lo que sugiere que habrían tenido elevada biomasa e importancia ecológica. Las hojas presentan la arquitectura bien conservada, pero carecen de cutículas o conexiones con estructuras reproductivas. Encontramos que los fósiles sólo se parecen superficialmente a *Celtis* y a taxones comparables de Cannabaceae, Ulmaceae, Rhamnaceae, Malvaceae, y muchas otras familias. Sin embargo, la morfología foliar distintiva se ajusta en detalle a *Dobinea* (Anacardiaceae), un género con dos especies de arbustos y grandes hierbas que se distribuye desde el Oriente de la India y el Tíbet hasta Myanmar y China central. Proponemos *Dobineaites ameghinoi* (E.W. Berry) gen et. comb. nov. para las hojas fósiles. Este hallazgo refuerza los ya extensos vínculos biogeográficos entre el Eoceno de Patagonia y Asia continental, proporciona el primer registro fósil relacionado con *Dobinea* y representa una rara presencia macrofósil gondwánica de Anacardiaceae, una familia que estaba muy extendida y diversificada en el hemisferio norte en ese momento. La diversa arquitectura foliar de las Anacardiaceae incluye varios patrones comúnmente asociados con otros grupos de plantas por lo que muchos fósiles de hojas de esta familia pueden permanecer aun mal identificados.

Palabras clave. Anacardiaceae. Argentina. Arquitectura foliar. *Dobinea*. Flora de China. Gondwana. Herbivoría. Laguna del Hunco.

THE EARLY EOCENE FOSSIL-LAKE BEDS at Laguna del Hunco in the Piedra Parada Caldera of northwestern Chubut, Argentina, contain a well-preserved, highly diverse plant and animal biota that has been known for a century (Clark, 1923; Berry, 1925; Dolgopol de Sáez, 1941). The pace of discovery has increased significantly over the past 25 years because of intensive, stratigraphically controlled collecting, resulting in over 8,000 specimens of more than 180 plant macrofossil species from more than 30 quarries in a 170 m stratigraphic section (*e.g.,* Wilf *et al.*, 2003, 2005a, 2023). More than 30 well-vetted plant families are present in the flora, including palynological occurrences (Barreda *et al.*, 2020).

Recent systematic work has vastly improved understanding of the floristic composition of the late-Gondwanan Laguna del Hunco flora and its biogeographic connections to living genera in South America, Africa, and especially Australasia and Southeast Asia (*e.g.,* Zamaloa *et al.*, 2006; Gandolfo *et al.*, 2011; Wilf *et al.*, 2013, 2019; Kooyman *et al.*, 2014). Most dominant plant species in the flora have been revised. For example, the second most abundant leaf species by field-census leaf counts, initially identified to the family Myrtaceae (Wilf *et al.,* 2005a), is now resolved in *Eucalyptus* and is associated with infructescences and flowers bearing in situ pollen of that genus (Gandolfo *et al.*, 2011; Hermsen *et al.*, 2012; Zamaloa *et al.*, 2020). The third most common, "*Tetracera*" *patagonica* leaves with putative affinities to Dilleniaceae (Berry, 1925), are fagaceous, now placed in *Castaneophyllum*, and associated with *Castanopsis* infructescences and dispersed castaneoid pollen (Wilf *et al.*, 2019; Barreda *et al.*, 2020). The seventh most abundant leaf type, the putative Cycadaceae "*Zamia tertiaria*," actually represents the araucarian conifer *Agathis*, supported by co-occurring *Agathis* pollen cones, seed cones, and ovuliferous complexes bearing in situ seeds (Wilf *et al.*, 2014; quotation marks indicate uncertain botanical affinities for a published name or other nomenclatural issues).

Despite these advances, the most common leaf species at Laguna del Hunco, "*Celtis*" *ameghinoi* E.W. Berry (1925), remains unrevised, leaving a gap in the fundamental knowledge of the assemblage and its paleoecology and biogeography. Notwithstanding its long collection history, the species is known only from leaf adpressions without cuticles, but its leaf architecture is well preserved.

Berry (1925) described "*Celtis*" "*ameghenoi*" based on three type specimens (Fig. 1) in the first report of plant fossils from Laguna del Hunco (also known then as El Mirador, Mirhoja, Laguna del Junco, and Laguna de los Huncos), from a small sample discovered by geologist Burton Clark (1923). The specific epithet honored this journal's namesake, Florentino Ameghino (1853–1911), whom Berry (1925: 200) referred to as "my lamented friend." Later, Berry (1938: 41) credited Ameghino for his initial inspiration to study South American geology and referred to "long drawn out discussions" about the ages of South American fossils. Berry (1938) corrected the typographic error in the species epithet as "*ameghinoi*," which we follow here.

The "*Celtis*" *ameghinoi* syntypes (Fig. 1) include one small leaf with a narrow, lanceolate aspect (Fig. 1.1) and two that are larger, wider, and cordate (Fig. 1.2, 1.3). Specimens since collected (Figs. 2–4) display a more complete spectrum of variation that encompasses the morphologies of the three types, sharing characters such as a pinnate, unlobed blade; prominent, closely spaced, irregular to compound teeth that occur on nearly all of the blade margin; secondary veins that increase in angle toward the base; widely spaced, weakly percurrent tertiary veins; and perpendicular vein branching from tooth principal veins to a vein knot just inside or at the tooth sinuses. Other common characteristics include a symmetrical ovate blade, cordate base (mostly on larger specimens), acute-to-acuminate apex, deflected major veins, and secondary veins that branch well inside the margin. The overall feature combination makes the species easily recognizable. Berry (1925) noted that "*C.*" *ameghinoi* was the most abundant form in the assemblage, which remains true today (Wilf *et al.*, 2005a). He (Berry, 1925: 198–199) considered the fossils "very well marked and characteristic of *Celtis*" (Cannabaceae, formerly in Ulmaceae and Celtidaceae), and he also found them similar to the New World genera *Momisia* (now a synonym of *Celtis*), *Trema* (Cannabaceae), and *Ampelocera* and *Phyllostylon* (Ulmaceae). Other genera that Berry listed as similar to the fossils were *Gouania* (Rhamnaceae) as well as *Grewia* and *Triumfetta* (both Malvaceae).

In his classic monograph of the middle Eocene (47.7 Ma; Wilf, 2012) Río Pichileufú flora from Río Negro province, Argentina, Berry (1938) reported but did not illustrate "*Celtis*" *ameghinoi* as a rare element. Rossetto-Harris (2023) re-examined the type and cohort Río Pichileufú collections that Berry studied (housed in the Division of Paleobotany, Smithsonian Institution, Washington, D.C.). She located four specimens labeled as "*Celtis ameghinoi*" in Berry's handwriting, finding that these specimens differ from the Laguna del Hunco type material and do not represent the same species.

Joaquín Frenguelli and Rodolfo Maldonado Bruzzone made significant early collections from Laguna del Hunco in the late 1930s and the early 1940s, housed at the Museo de La Plata (*e.g.,* Frenguelli, 1943a, 1943b). Traverso (1951) described ca. 60 specimens of "*Celtis*" *ameghinoi* from these collections in an unpublished thesis. Many years later, González (2008), also in an unpublished thesis, made the only other taxonomic interpretations of "*Celtis*" *ameghinoi* to date. She studied the species using fossil collections housed at several institutions from Laguna del Hunco and Arroyo Chacay, an Eocene site in Río Negro Province (*e.g.,* Machado *et al.*, 2023). In preparing the present manuscript, we found the Arroyo Chacay material to represent another species; thus, we consider Laguna del Hunco to be the only known site where "*Celtis*" *ameghinoi* occurs. González (2008) concluded that "*C.*" *ameghinoi* differed substantially from all the living genera that she compared, including extant *Celtis*, *Trema*, *Aphananthe*, and *Phyllostylon* (see Discussion for updated comparisons incorporating these observations).

"*Celtis*" *ameghinoi* is occasionally referenced as a true representative of *Celtis* (*e.g.,* Barreda & Palazzesi, 2007, 2010; Vento & Prámparo, 2018; Romero-Lebrón *et al.*, 2020).

More often, it serves as a morphotype in paleoecological analyses. From field-census data, "*C.*" *ameghinoi* leaves were the most abundant fossils across all quarries at Laguna del Hunco, accounting for 597 of the 4,303 total specimens (13.9%; Wilf *et al.*, 2005a). The species also had the highest leaf counts at two of the four principal census quarries (21.7% at LH02 and 27.6% at LH04; *Eucalyptus frenguelliana* was dominant at the other two). Based on modern analog studies, ranked leaf counts correlate well with ranked source biomass by species (Burnham *et al.*, 1992; Burnham, 1997), implying a high biomass of the source plants. From the same field census, "*C.*" *ameghinoi* showed insect damage in 12.5% of leaves (Wilf *et al.*, 2005b) and a substantial diversity of 26 damage types (DTs; Labandeira *et al.*, 2007) across all functional groups: external feeding, piercing-and-sucking, galling, mining, and oviposition. Two mining occurrences on "*C.*" *ameghinoi* were illustrated as exemplar specimens of DT91 and DT93 in the standard guide for fossil insect damage (Labandeira *et al.*, 2007; Fig. 4.6–4.8). Some oviposition damage (Fig. 4.9) was subsequently described under the ichnospecies *Paleovoidus arcuatum* (Sarzetti *et al.*, 2009) and further analyzed morphometrically and behaviorally (Romero-Lebrón *et al.*, 2020, 2023). Its elevated abundance, diverse insect damage, and unknown biogeographic relationships all highlight the significance of understanding the botanical affinities of "*Celtis*" *ameghinoi*.

Taxonomic descriptions of isolated leaf taxa without cuticles have well-known caveats, especially when based on superficial comparisons with living genera, as historically practiced (see Dilcher, 1971; Hill, 1982). However, leaf fossils that are described using a full suite of well-defined leaf-architectural characters (Ellis *et al.*, 2009) and compared carefully with living analogs advance our understanding much more than historical names in scare quotes or informal, often unillustrated morphotypes. Several angiosperm leaf taxa with no associated reproductive organs have been described from Laguna del Hunco, including species of *Akania* (Akaniaceae), *Ripogonum* (Ripogonaceae), Proteaceae, Atherospermataceae, and Monimiaceae (Romero & Hickey, 1976; González *et al.*, 2007; Knight & Wilf, 2013; Carpenter *et al.*, 2014). Leaves from the site that are associated with, but not attached to, related reproductive organs include species of *Eucalyptus* (Myrtaceae), *Macaranga* (Euphorbiaceae), castaneoid Fagaceae, and Menispermaceae (Gandolfo *et al.*, 2011; Jud *et al.*, 2018; Wilf *et al.*, 2019, 2023). Here, we present compelling similarities of the "*C.*" *ameghinoi* fossils to an unexpected group, the Anacardiaceae, particularly the living Chinese species *Dobinea delavayi.* We consider the implications of our results for the paleoecology of Laguna del Hunco, biogeographic connections of late-Gondwanan Patagonia, and the fossil history of Anacardiaceae.

Institutional abbreviations. Acronyms for repositories and their corresponding institutions (when distinct) denote individual specimens or institutions, respectively. **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (institutional acronym **NMNH**); **MPEF-Pb,** Paleobotanical Collection of Museo Paleontológico Egidio Feruglio, Trelew, Argentina (**MEF**); **LPPB,** Paleobotanical Collection of Museo de La Plata, La Plata, Argentina (**MLP**); **BA-Pb,** Paleobotanical Collection of Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (**MACN**); **MJHG,** Museo Jorge H. Gerhold, Ingeniero Jacobacci, Argentina; **LILPB,** Paleobotanical Collection of Fundación Miguel Lillo, Tucumán, Argentina (**LIL**); **K,** Royal Botanic Gardens, Kew, UK; **BAB,** Instituto Nacional de Tecnología Agropecuaria, Castelar, Argentina; **SI,** Instituto de Botánica Darwinion, San Isidro, Argentina; **CTES,** Instituto de Botánica del Nordeste, Corrientes, Argentina; **BH,** L.H. Bailey Hortorium, Cornell University, Ithaca, USA; **L,** Naturalis Biodiversity Center, Leiden, The Netherlands; **US,** United States National Herbarium of the Smithsonian Institution, Washington, D.C., USA; **P,** Muséum National d'Histoire Naturelle (**MNHN**), Paris Herbarium, France; **NY,** New York Botanical Garden, New York, USA. Several additional herbaria mentioned in the text are cited by their standard acronyms according to the Index Herbariorum, https://sweetgum.nybg.org/science/ih.

MATERIALS AND METHODS

All fossils discussed here came from the Tufolitas Laguna del Hunco, a unit of mixed siliciclastic-volcaniclastic fossil-lake beds of the Eocene Huitrera Formation in the middle Río Chubut region of northwest Chubut, Argentina (Petersen, 1946; Aragón & Mazzoni, 1997; Gosses *et al.*, 2021). The Tufolitas record rapid infilling of the subsiding Piedra Parada Caldera following a series of massive eruptions (estimated >300 km^3 emplacement) recorded in the underlying Ignimbrita Barda Colorada (IBC; Aragón *et al.*, 2018). The Tufolitas are exposed throughout the extensive caldera (ca. 30 km in diameter). The strata are visually spectacular; they weather a brilliant white and are underlain by thick ignimbrites, intruded by extensive dikes and laccoliths, and capped with basalt flows (Petersen, 1946; Aragón & Mazzoni, 1997; Aragón *et al.*, 2001, 2004).

Fossil preservation in the Tufolitas is outstanding along a 1.3-km long escarpment in its northeastern exposures near Cerro Mirador at Laguna del Hunco ("Lake of Rushes," a small playa lake), possibly because of reduced igneous disturbance of the strata in the area. Jason Hicks (in Wilf *et al.*, 2003) established a 170 m composite stratigraphic section of the Tufolitas at Laguna del Hunco, incorporating 25 fossil quarries (LH01–LH25), two paleomagnetic reversals, and three ^{40}Ar/^{39}Ar dated primary airfall tuffs. Additionally, the youngest ignimbrites in the IBC have an ^{40}Ar/^{39}Ar age of 52.54 ± 0.17 Ma, which provides a maximum age for all fossils found in the superposed Tufolitas (Gosses *et al.*, 2021). As most recently summarized elsewhere from these and other constraints (Gosses *et al.*, 2021; Wilf *et al.*, 2023), all fossils at Laguna del Hunco date to the interval 52.2–52.0 Ma, coinciding with the early Eocene climatic optimum and the final stages of Gondwana. The paleoenvironment is well established as an everwet (perhumid), mesic, lake-margin rainforest, based on the documented drought tolerances and climatic ranges of the living relatives of the fossil plants (*e.g.,* Wilf, 2012; Merkhofer *et al.,* 2015) and the preservation of extraordinarily drought-sensitive accessory transfusion tissue in the leaves of the fossil podocarp conifer *Acmopyle grayae* (Andruchow-Colombo *et al.,* 2023).

Several collections have been made at Laguna del Hunco over the past century; however, until comparatively recently (Wilf *et al.*, 2003), no precise locality data have been recorded. Many older collections appear to have the characteristic lithology of quarry LH04 of Wilf et al. (2003), the most accessible site and the only location we have seen showing definite evidence of prior excavations (Wilf, 2020). The three syntypes of "*Celtis*" *ameghinoi* (Fig. 1) are now housed in the Laguna del Hunco type collection (Berry, 1925) at NMNH. Subsequent collections were made for several Argentine institutions, including MLP, the University of Buenos Aires (made by Edgardo Romero, currently uncatalogued), MACN (E. Romero), MJHG (made by Rodolfo Casamiquela, see Wilf *et al.* 2023), LIL, and MEF.

Since the late 1990s, international expeditions to Laguna de Hunco have been launched from the MEF, leading to extensive collections tied to precise stratigraphy and age control that have supported most subsequent research on the site (Wilf *et al.*, 2003, 2005a). Field censuses of 4,303 total specimens from 25 individual quarries (LH01–LH25) in 1999 and 2002 (Wilf *et al.*, 2003, 2005a) established the high abundance of "*C.*" *ameghinoi* fossils (see Introduction). Additional material of the species was collected during several subsequent MEF field expeditions, including two newer quarries, LH27 and LH29 (see Gandolfo *et al.*, 2011; Deanna *et al.*, 2020).

A total of 280 specimens of "*C.*" *ameghinoi* were studied at NMNH, MEF, MLP, LIL, MACN, and (by A. Iglesias, see Acknowledgments; Fig. 3.12) MJHG. At least 50 additional specimens that remain uncatalogued and unavailable for validation are held at the University of Buenos Aires. Photography began in the late 1990s and involved a series of film and digital cameras. More recently, Nikon D90, D700, and D850 DSLRs with 60 mm and 105 mm macro lenses and polarizing filters have been used. Due to the lack of cuticular or other micromorphological preservation, little microscope photography was required. A library containing original-resolution images of the fossils, a specimen list, and high-resolution versions of Figures 1–4 is deposited on Figshare at https://doi.org/10.6084/m9.figshare.24451249.

The extant material consulted included the recent open-access digital compilation of more than 26,000 cleared and x-rayed leaves and many of the corresponding physical slides, representing more than 350 families and 4,500 genera in total (Wilf *et al.*, 2021; Fig. 5). Herbarium surveys by CCG at BAB, SI, CTES, BH, and US extensively covered the comparable genera of Cannabaceae and Ulmaceae. We also used several online herbaria to examine relevant taxa (Fig. 6), including those of L, https://bioportal.naturalis.nl, US, https://collections.nmnh.si.edu/search/botany, P, https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form, and NY via the C. V. Starr Virtual Herbarium, http://sweetgum.nybg.org/science/vh. Aggregator sites included the Chinese Virtual Herbarium, https://www.cvh.ac.cn, and JSTOR Global Plants, https://plants.jstor.org. For Anacardiaceae, additional sources included the literature (especially Gentry, 1993; Martínez-Millán & Cevallos-Ferriz, 2005; Ming & Barfod, 2008; Andrés-Hernández & Terrazas, 2009; Pell *et al.*, 2010; Zich *et al.*, 2020; Mitchell *et al.*, 2022) and inspection of *Dobinea* species by T. Wang at K (see Acknowledgments; Fig. 6.2).

For increased readability, taxonomic authorities are only provided in the text where necessary to support new taxonomic descriptions. However, all nomenclature and use of authorities for extant taxa follow standard compilations, including Tropicos, https://www.tropicos.org, World Flora Online, https://www.worldfloraonline.org, and Kew's Plants of the World Online, https://powo.science.kew.org. Authorities for fossil taxa can be found in the corresponding cited literature. Leaf-architectural terminology follows Ellis et al. (2009).

SYSTEMATIC PALEONTOLOGY

Family ANACARDIACEAE R. Brown, 1818: 431

Genus *Dobineaites* Wilf, C. González, Gandolfo & Zamaloa gen. nov.

Generic diagnosis. Leaves opposite, simple, petiolate. Blade ovate, unlobed, usually symmetrical; primary venation pinnate, deflected. Secondary veins craspedodromous, dichotomizing laterally; secondaries increase in angle and decrease in spacing basally. Agrophic veins compound, the first set expressed only along the basal margin. Tertiary veins thick, moderately and irregularly spaced, weakly to strongly opposite percurrent, angle increasing basally. Margin serrate; teeth prominent, closely spaced, continuous nearly to the blade base. Teeth simple or compound, apex simple and apiculate, sinuses angular, principal vein medial and prominent with near-perpendicular branches to vein junctions near or at the sinuses.

Type species. ***Dobineaites ameghinoi*** (E.W. Berry) Wilf, C. González, Gandolfo & Zamaloa comb. nov.

Figures 1–4

Basionym. *Celtis ameghenoi* E.W. Berry, 1925, *Johns Hopkins University Studies in Geology 6*:198.

Lectotype here designated. USNM 222678 (Fig. 1.1). Tufolitas Laguna del Hunco, Huitrera Formation, early Eocene (Ypresian), collected in the early 1920s by Burton Clark, exact date and collection site unknown.

Syntypes. USNM 222679 (Fig. 1.2), USNM 222680 (Fig. 1.3); provenance as for the lectotype.

Referred material (277 specimens). From quarry LH01: MPEF-Pb 7700, 7701. From LH02: MPEF-Pb 1053, 3168, 7702–7725, 7794–7818. From LH03: MPEF-Pb 7726, 7727. From LH04: MPEF-Pb 995, 2329, 3169, 7728–7762, 7819–7839, 7858–7864, 7870, 7871, 7881–7895. From LH06: MPEF-Pb 7763–7769, 7840–7846. From LH08: MPEF-Pb 7770. From LH13: MPEF-Pb 3171, 7771–7776, 7847–7854, 7896, 7897. From LH15: MPEF-Pb 7777, 7865. From LH16: MPEF-Pb 7778, 7779, 7907. From LH17: MPEF-Pb 7780–7787. 7855–7857. From LH18: MPEF-Pb 7788. From LH20: MPEF-Pb 7789. From LH22: MPEF-Pb 7790. From LH23: MPEF-Pb 7791, 7792. From LH25: MPEF-Pb 7866–7872. From LH27: MPEF-Pb 7869, 7873–7879, 7898. From LH29: MPEF-Pb 7899–7901. From float, unknown, or out-of-section locations (at MEF): MPEF-Pb 1449, 1450, 7793, 7880, 7902–7906. Exact collection site unknown, other: BA-Pb 12633; MJHG 45Pb–53Pb; Lil-Pb 5815, 5825, 5913, 5920, 5931; LPPB 739, 741–746, 749, 759–762, 765–767, 773, 775, 781, 782, 898, 920, 943, 2470–2472, 2475–2477, 2483–2485, 2487, 2490, 2492, 2497–2502, 2504, 2506, 20417, 20418, 20420, 20437.

Emended specific description. Leaves (Figs. 1–4) are opposite (Fig. 4.1–4.4), simple, and petiolate with marginal insertion. The lamina is unlobed, and the margin is strongly serrate. Petioles are eight to >23 mm in length and 0.8–2.0 mm wide. Laminar size (from Merkhofer *et al.* 2015, $n = 101$) is 75–15,000 mm^2 (nanophyll to mesophyll), with a mean area of 1133 mm^2 (based on means of natural logs; microphyll). Laminar length is 2.5–14.5 cm, width is 1.0–10.2 cm, and length-width ratio is 1.1–2.9:1. Small axillary leaves are present (Fig. 4.1–4.4). The blade shape is ovate to lanceolate (Fig. 3.11), sometimes elliptic (Fig. 4.5), and symmetrical or slightly asymmetrical basally (*e.g.,* Fig. 3.1). The base is convex to slightly cordate (*e.g.,* Fig. 2.2) but may be cuneate (Fig. 3.12); the base angle is variably acute or obtuse. The apex shape is usually straight to slightly acuminate, sometimes convex, and the angle is acute. The overall leaf form varies with size (Figs. 1–3). Smaller leaves, such as the lectotype (Fig. 1.1), more often have a non-cordate base, ovate-lanceolate shape, and higher aspect ratios; larger leaves, such as the syntypes (Fig. 1.2, 1.3) tend to have broad-ovate blades with cordate bases and lower aspect ratios (*e.g.,* Fig. 2.1).

Primary venation is pinnate, and the midvein course is often deflected at secondary junctions. Secondary veins are decurrent in ca. 5–10 offset pairs, craspedodromous, and dichotomize up to 3–4 times. The secondary course is weak, moderately recurved, and often slightly deflected at junctions with minor secondary and tertiary veins. Secondary spacing decreases, and the secondary angle markedly increases basally (from ca. 35–55° to 70–100°). Most leaves have one or more abruptly thinner, high-angled or obtuse basal secondary pairs that diverge near the petiole insertion (*e.g.,* Fig. 2.2, Fig. 3.3). Agrophic veins are usually compound, and the first agrophic complex is restricted to a small area near the basal margin of the blade because of the high-angled basal secondaries that limit its potential extent. The major and minor secondaries terminate at the tooth apex, often with perpendicular tertiary branches to vein junctions (vein knots) near or at the nadirs of the sinuses. A thin fimbrial vein is present (Fig. 2.3). Intersecondary veins are absent.

Tertiary venation (*e.g.,* Figs. 2.2, 3.4) is moderately spaced, thick, and usually weakly opposite percurrent but may be mixed percurrent or reticulate. The tertiary spacing and angle are irregular. The departure of percurrent tertiaries from the midvein and major secondaries is generally perpendicular but inconsistently obtuse or acute. The tertiary angle to the midvein markedly increases toward the base. The tertiary course is usually convex but may be straight or sinuous or form a concentric pattern near the base. The tertiary distal course is basiflexed, and the junction with the subjacent secondaries is generally perpendicular. Tertiaries that reach the margin terminate in the tooth apices or vein knots located at or near the sinuses (Fig. 2.3). The quaternary venation is weakly mixed percurrent to irregular reticulate, and the quinternary venation is regular to irregular reticulate. Areolation is well developed, with freely ending veinlets mostly one-branched at the sixth order.

The teeth (*e.g.,* Fig. 2.3) are irregular in size and always prominent, projecting from the margin up to 4.4 mm (measured medially from the tooth apex to a line projected orthogonally from the basal sinus nadir). Teeth are present continuously over nearly the full blade margin, and the only untoothed area is the immediate vicinity of the petiole insertion. The teeth are simple or once compound, closely spaced (ca. 2–7 major teeth per cm), with angular sinuses. The tooth shape is generally flexuous with an apiculate apex; flank shapes include flexuous/flexuous, flexuous/convex, straight/flexuous, convex/convex, straight/straight (triangular aspect), or straight/convex. The tooth apex is apiculate and simple (non-glandular; Fig. 2.3). The principal vein is a major secondary, minor secondary, or exterior tertiary vein that is usually deflected by vein junctions before entering the tooth. The principal vein is medial and prominent, and its course is slightly curved, basally deflected, or nearly straight. The accessory veins emerge roughly perpendicular to the principal vein and form irregular loops, reticulate, or run toward the adjacent sinus nadir, joining a knot with other minor veins.

The insect damage types (Figs. 2.5, 3, 4.5–4.8) previously recorded (Wilf *et al.*, 2005b; Labandeira *et al.*, 2007; Sarzetti *et al.*, 2009) include external feeding (DTs 1–5, 7, 12–17, 22, 26, 29, 57), piercing-and-sucking (DT46), galling (DTs 32–34), mining (DTs 41, 90, 91), and oviposition (DTs 54, 76), to which we add an occurrence of mining DT93 on a specimen here identified to the species (Fig. 4.6, 4.7).

DISCUSSION

Affinities of *Dobineaites ameghinoi* comb. nov.

The characters of the fossils observed in the three type specimens (Fig. 1) are consistent with hundreds of subsequently collected fossils (Figs. 2–4), which fill the morphological continuum between the types (Fig. 1) and support Berry's (1925) hypothesis of a single species. Despite the elevated diversity of the Laguna del Hunco leaf flora, *Dobineaites ameghinoi* is rapidly identifiable based on the combination of obtuse basal secondary veins and prominent, densely spaced, apiculate, often flexuous, frequently compound teeth with non-glandular apices. The fossils can often be confidently identified even without the margin or base preserved (*e.g.,* Fig. 4.6) because of their distinctive deflected major veins, branching secondaries, and thick, usually weakly opposite percurrent, irregularly spaced, and angled tertiaries.

Our leaf architectural survey indicates that all groups previously considered for the fossils (*e.g.,* Berry, 1925) have only superficial similarities, such as the presence of an ovate blade and large or compound teeth in some species. Due to the substantial number of compared taxa and the low similarity of nearly all of them to the fossils, we expedite the discussion below using a set of cleared leaf exemplars as visual references (Fig. 5).

Despite their basionym, the fossils only superficially resemble *Celtis* (Fig. 5.1, 5.2). *Celtis* leaves are alternate and often have markedly asymmetrical petiole insertions and laminae, unlike the fossils; the primaries may be pinnate like the fossils or palmate, usually with three primaries. The basal pair of *Celtis* lateral primaries or secondaries is robust, often runs on (naked basal veins) or close to the margin near the petiole insertion, and is usually abruptly acute, set well below the next set of secondaries and generating prominent agrophic veins that extend well up the blade. This architecture contrasts sharply with the secondaries that basally decrease in spacing and increase in angle in the fossils (Figs. 2–4), leaving little space for the basalmost set of agrophic veins to develop. *Celtis* secondary veins usually loop inside the margin (Manchester *et al.*, 2002), unlike the craspedodromous secondary veins of the fossils. *Celtis* leaves may be toothed or entire; however, when present, *Celtis* teeth are not usually compound and never markedly compound like the fossils. This discussion also applies to other Cannabaceae genera with comparable leaves (Fig. 5.3–5.5), such as *Aphananthe*, *Lozanella*, *Pteroceltis*, and *Trema*. Thus, we can confidently eliminate affinities of the fossils to Cannabaceae. The only remaining South American *Celtis* fossils that are still valid (*e.g.,* Manchester *et al.*, 2002) appear to be well-preserved *C. santosi* endocarps from the Paleogene Itaboraí beds in Rio de Janeiro State, Brazil (Beurlen & Sommer, 1954).

Regarding Ulmaceae, Berry (1925) mentioned *Ampelocera* (Fig. 5.8) and *Phyllostylon*, but neither has many comparable features. Some Moraceae (*Morus*, *Broussonetia*) and Urticaceae (*Boehmeria*, *Leucosyke*) have species with similar leaves to the fossils, such as large, compound, or densely spaced teeth; however, they also have markedly acute, robust basal secondaries and several other differences (Fig. 5.6, 5.7). In Rhamnaceae, leaves most like the fossils typically have markedly acute, robust basal secondaries (or acrodromous lateral primaries) that run close to or on the margin, set back from the next pair, and generate well-developed agrophic veins over much of the blade, unlike the high-angled, crowded, weak basal secondaries and reduced agrophic veins in the fossils. Rhamnaceae secondary veins are strong, regular, and smoothly recurved apically rather than deflected like the fossils; when present, the teeth are often reduced and glandular and rarely compound like the fossils. Examples include the ziziphoid genera *Gouania* (Fig. 5.9), *Ceanothus*, and *Paliurus*, which also have distinctive interior secondary venation not seen in these fossils (see Wilf et al. 2022), as well as *Colubrina*, *Hovenia*, and *Ziziphus*.

In Rosaceae, many genera have species with large, densely spaced teeth superficially similar to the fossils but few other shared features. *Rhodotypos scandens* (the sole species of its genus, with opposite leaves) and *Rubus* species (Fig. 5.10, 5.11) have obtuse basal secondaries and compound teeth; however, the secondary veins are more numerous and regular and less deflected, and the often-glandular teeth do not resemble the fossils. Moreover, *Rubus* species frequently have compound leaves and lobed leaf blades. Other families of Rosales (as defined in Chase *et al.*, 2016) show no significant similarities to the fossils, which also lack the characteristic glandular teeth that are widespread in the order (Hickey & Wolfe, 1975). We conclude that the fossils do not belong to Rosales as long suggested (Berry, 1925).

Outside Rosales, the leaves of some Euphorbiaceae species (Malpighiales; Fig. 5.12) show only a superficial resemblance to the fossils. Malvaceae (Malvales) is also not suitable for this material. The family tends to have alternate leaves as well as higher-ranked leaf organization and other features that are unlike the fossils, such as palmate venation with strong, markedly acute lateral primary veins or basal secondaries that emerge from the base; well-developed and organized agrophic veins; and thin, closely spaced, regularly opposite percurrent tertiaries (Hickey & Wolfe, 1975; Carvalho *et al.*, 2011; Wilf *et al.*, 2022). This syndrome includes the taxa mentioned by Berry (1925), *Triumfetta* and *Grewia* (Fig. 5.14, 5.15), and many others such as *Melochia* (Fig. 5.13).

In Sapindales, entire-margined, compound-leaved taxa are prevalent, and very few species remotely resemble the toothed, simple-leaved fossils. Some maples have some similarities, such as *Acer tataricum* (Sapindaceae; Fig. 5.16), which has simple, lobed or unlobed, cordate-ovate leaves and compound teeth. However, among other differences, analogs of the frequent shallow to more incised lobes would be apparent in the large sample size of the fossil species. Partial similarities to the fossils occur in some species of *Bursera* (Burseraceae, *e.g., B. epinnata*) and *Brucea* (Simaroubaceae).

Like the other sapindalean families, the Anacardiaceae usually display entirely dissimilar leaf architecture to these fossils, as described in surveys (Martínez-Millán & Cevallos-Ferriz, 2005; Andrés-Hernández & Terrazas, 2009; Mitchell *et al.*, 2022). Many of the more than 870 Anacardiaceae species have alternate, compound leaves with a characteristic general appearance of the leaflets that is unlike the fossils, including various combinations of asymmetrical blades (usually due to compound leaf organization), irregular cladodromous or craspedodromous secondaries, secondaries and intersecondaries that terminate in tooth sinuses, ramified to elaborately ramified tertiary veins, and irregularly sized teeth when present. There are seven genera (*Schinus, Lithraea, Mauria, Astronium, Loxopterygium, Myracrodruon,* and *Schinopsis*) of the family in Argentina, none of which resembles the fossils (but see Passalia *et al.*, 2019 for Miocene *Lithraea*). However, the leaf architecture of Anacardiaceae encompasses diverse forms similar to other plant groups, and many fossils of the family probably remain unrecognized for this reason (e.g., Passalia *et al.*, 2019). These include clusioid venation in species of *Ozoroa* and *Abrahamia* (which usually have some degree of cladodromous secondary branching and ramified tertiaries); Myrtaceae-like architecture in several *Spondias* species (which have asymmetrical blades and some ramifications of the tertiaries); and several architectural similarities with the closely related families Sapindaceae and Burseraceae as well as Lauraceae, in the case of simple-leaved Anacardiaceae (Gentry, 1993). Only a few genera of Anacardiaceae have species with simple, toothed leaves, such as *Cotinus*, *Rhus*, and *Schinus* (the range of *S. roigii* includes the Laguna del Hunco site), none of which resembles the fossils, and *Dobinea* Buchanan-Hamilton (1825) ex D. Don (Figs. 5.17, 6), whose leaves provide unexpected and compelling similarities.

Dobinea is a dioecious Asian genus containing two species. The type species, *D. vulgari*s Buchanan-Hamilton (1825) ex D. Don., is opposite-leaved like the fossils but entirely dissimilar in leaf architecture (Fig. 6.4), whereas *D. delavayi* (Baillon) Baillon (1890), is alternate-leaved, like most Anacardiaceae species, but has leaf architecture identical to that of the fossils (Figs. 5.17, 6.1–6.3; Wu, 1979, 1986; Ming & Barfod, 2008). *Dobinea vulgaris* is a hill-forest dwarf shrub (elevation 1300-1400 m) with a broad, generally subtropical range, including Bangladesh, Assam, and the eastern Himalaya to south-central China and Myanmar, whereas *D. delavayi* is a perennial shrub-like herb with a more temperate, restricted distribution in grasslands and woodlands at 1100-2300 m elevation in southwestern Sichuan and central northwestern Yunnan (Ming, 1980; Ming & Barfod, 2008). Ming (1980) considered south-central China the likely area of origin for several anacardiaceous genera, including *Dobinea*. The most conspicuous feature of this genus, not yet observed in the fossil record, is its terminal female inflorescence containing accrescent, foliose, papery bracts. The bracts have venation and teeth similar to the regular leaves but include several sets of obtuse basal secondary veins. The pedicel is adnate to the bract midvein and bears unicarpellate, perianth-free flowers and subsequent small fruits (Fig. 6.1; Baillon, 1887; Engler, 1896; Ming & Barfod, 2008; Pell *et al.*, 2010). These elm-like winged fruits enable wind dispersal, and the genus is wind-pollinated, which is unusual in the Anacardiaceae (Pell *et al.*, 2010).

The systematic placement of *Dobinea* has varied historically among a separate family (Podoaceae, along with *Campylopetalum*, a monotypic herb endemic to Thailand), Sapindaceae (as a member of the former Aceraceae), and Anacardiaceae. Molecular analyses have resolved the two species of *Dobinea* as a monophyletic group in Anacardiaceae, estimated the species divergence at ca. 10.8 Ma, and estimated the genus divergence as 40–50 Ma, similar to the age of these fossils (Pan *et al.*, 2008; Pell *et al.*, 2010; Weeks *et al.*, 2014; Liu *et al.*, 2021; Joyce *et al.*, 2023). *Campylopetalum* has resolved as a sister genus to *Dobinea* (Weeks *et al.*, 2014; Joyce *et al.*, 2023), and the two genera together resolved as sister to the large A2 clade of Joyce *et al.* (2023; the A2 clade is equivalent to the Anacardioideae with *Campnosperma* removed). *Campylopetalum* and *Dobinea* share winged fruits, chromosome number (n = 7), and several pollen characters, such as a small overall size of ca. 10–15 µm, suboblate-oblate spheroidal shape, three (four) compound apertures, and exine with reticulate sculpture (Erdtman, 1952; Forman, 1953; Pell *et al.*, 2010).

Comparisons of vegetative characters show close similarities between the fossils and *Dobinea* (Figs. 5.17, 6), especially *D. delavayi* (羊角天麻, roughly translated as Goat's Horn Weed). Stipules are absent in *Dobinea*, as for Anacardiaceae as a whole (Pell *et al.*, 2010); however, we observed stipule-like small or immature leaves that are often present on axils or axillary shoots in both extant species (Fig. 6.3, 6.4) and the fossils (Fig. 4.1–4.4). *Dobinea* leaves are simple, petiolate, unlobed, toothed, and either opposite, with rounded to cuneate bases, oblong to lanceolate blade shape, and a regularly serrulate margin (*D. vulgaris*), or alternate, with cordate to convex bases, ovate to lanceolate blade shape, acuminate apex, and an irregularly serrated margin, the leaf size decreasing markedly along the shoot (*D. delavayi*; Fig. 6.1, 6.3; Baillon, 1887; Wu, 1986, 1988; Ming & Barfod, 2008). Interestingly, in the basionym description of the species (as *Podoon delavayi* Baillon), Baillon (1887: 682) noted, "*Ses organes de végétation sont ceux d'un* Morus *ou d'un* Celtis" (its vegetative organs are those of a *Morus* or a *Celtis*).

Like *D. delavayi*, the fossil leaves are petiolate, symmetrical, or slightly asymmetrical at the base. In both the fossil and living species, the primary and secondary venation is weak and frequently deflected; there is usually a thin, basal pair of secondaries diverging near the petiole insertion, the secondaries are craspedodromous and often dichotomize inside the margin, intersecondaries are absent, and the secondary vein angle increases markedly towards the base. Agrophic veins are compound and slightly irregular, and the high-angled basal secondaries restrict the basalmost set to a small portion of the basal margin. Tertiary veins are weakly percurrent, moderately and irregularly spaced, and become more obtuse basally. Higher-order venation is reticulate, and mostly once-branched freely ending veinlets are present. The tooth features are also the same (*e.g.,* Fig. 6.2), including coverage nearly to the blade base, close spacing, irregular sizes, angular sinuses, simple or compound organization, flexuous and other flank shapes, and non-glandular, apiculate apices (which appear thickened due to abrupt apical narrowing around the principal vein but have no glandular tissue). The tooth venation includes a prominent medial vein that generates perpendicular branches to vein knots inside or at the sinuses.

Additional features of the fossils are also consistent with *Dobinea delavayi*. With decreasing blade size, the fossils generally show increasing aspect ratios and a gradation from cordate to ovate-lanceolate blade shapes (*e.g.,* Fig. 3), as seen distally along single branches of *D. delavayi* (Fig. 6.1). Moreover, the discovery of a single fossil specimen with attached leaves (Fig. 4.1–4.4) confirms that the fossil species had simple leaves and shows small axillary leaves, a feature often seen in both living *Dobinea* species (Fig. 6.3, 6.4). Perhaps the only difference between the fossils and *D. delavayi* is that the fossil leaves are opposite (Fig.

4.1), a rare trait in Anacardiaceae that nonetheless occurs in the other living species in the genus (*D. vulgaris*). We conclude that the fossil leaves of *D. ameghinoi* are strikingly similar to those of extant *D. delavayi* and only superficially comparable with the other taxa examined (Fig. 5), which nearly all have strong, acute lateral primaries or secondaries emerging from the petiole insertion (vs. obtuse, weak basal secondaries in the fossils) and robust major-vein courses (vs. deflected major veins and bifurcating secondaries in the fossils).

Although we consider the leaf fossils to be closely related to living *Dobinea*, we maintain caution by placing them in the new extinct genus *Dobinaeites* due to the absence to date of other evidence for *Dobinea* at the site, including the distinctive winged fruits (Fig. 6.1). *Dobinea*-like pollen (Radlkofer, 1888; Erdtman, 1952; Forman, 1953) was also not found in the dispersed associated palynoflora (Barreda *et al.*, 2020), although Anacardiaceae grains are rare in the assemblage overall, and many other abundant macrofossil taxa in the flora are not yet matched with associated palynotaxa (Barreda *et al.*, 2020). More circumstantially, the impressive abundance of the fossil leaves, suggesting high biomass, as discussed earlier, appears to be inconsistent with the herb and shrub habits of the living *Dobinea* species.

Contribution to the Anacardiaceae fossil record

Dobineaites ameghinoi fossils from Laguna del Hunco represent a rare macrofossil occurrence of Anacardiaceae in Gondwana, the first report of a fossil allied with *Dobinea*, and one of the few fossil occurrences affiliated with living Asian-endemic Anacardiaceae. The Anacardiaceae have a rich macrofossil record, especially from the Eocene onwards in North America and Europe (*e.g.,* Manchester, 1999; Manchester *et al.*, 2009; Herrera *et al.*, 2012; Mitchell *et al.*, 2022; Del Rio *et al.*, 2023; Joyce *et al.*, 2023), but they have little representation in Gondwana. Examples of numerous Laurasian Paleogene occurrences based on reproductive materials include fossil cashew nuts (*Anacardium*) with characteristic inflated hypocarps from the middle Eocene Messel locality (Germany; Manchester *et al.*, 2007), the extinct fruit genus *Pentoperculum* (Spondeae) from the early Eocene London Clay and the middle Eocene Clarno flora of Oregon (Reid & Chandler, 1933; Manchester, 1994), and *Rhus* fruits from Clarno (Manchester & Judd, 2022). *Rhus* has a rich record of fossil leaves since the Eocene, although much of the foliage may belong to extinct genera (Manchester & Judd, 2022). Paleogene leaf records attributed to *Rhus* and other genera mostly come from several Eocene sites in the western USA and the Oligocene of Puebla, Mexico (*e.g.,* MacGinitie, 1953, 1969; Wolfe & Wehr, 1987; Meyer & Manchester, 1997; Manchester, 2001; Ramírez & Cevallos-Ferriz, 2002; Flynn *et al.*, 2019; Mitchell *et al.*, 2022). Reliable fossil evidence for living endemic genera of Asian Anacardiaceae includes *Choerospondias* endocarps from the London Clay and several Oligocene and younger sites in Eastern Europe, China, and Japan (summarized by Manchester *et al.*, 2009; Wang *et al.*, 2020), along with *Dracontomelon* endocarps from the late Eocene of Panamá (Herrera *et al.*, 2012).

There are almost no macrofossil records of Anacardiaceae in the Southern Hemisphere outside of South America. One important exception is fossil wood consistent with the Anacardioideae subfamily (*Anacardioxylon semecarpoides*; Wheeler *et al.*, 2017) from the ca. 66 Ma Deccan sequence in Maharashtra, India, which was located in the Southern Hemisphere tropics at the time, long after India had separated from Gondwana. Several palynological occurrences have been resolved at the family level in Australia (*e.g.,* compilation in Kooyman *et al.*, 2014).

In Gondwanan South America, putative occurrences of *Anacardium* nuts from Perú, Ecuador, and Colombia, also reported by Berry in the 1920s (Berry, 1924a, 1924b, 1929a, 1929b), are doubtful because of the lack of attached hypocarps (Manchester *et al.*, 2007). As reviewed by Burnham and Carranco (2004), there are numerous historical reports of putative fossil anacardiaceous foliage from several South American countries that should be considered unconfirmed, including "*Schinopsis*" *patagonica* from Laguna del Hunco (Berry, 1925) and several species from Río Pichileufú (Berry, 1938). Post-Gondwanan occurrences in northern South America include fossil wood with features of *Anacardium* and *Mangifera* from the late Eocene Piedra Chamana Fossil Forest of Perú (Woodcock *et al.*, 2017) and a winged fruit of *Loxopterygium* from Ecuador (Burnham & Carranco, 2004).

Nevertheless, there is growing evidence for the presence of Anacardiaceae in southern South America since the early Paleocene. At Laguna del Hunco, supporting data include pollen occurrences of the family mentioned earlier (Barreda *et al.*, 2020) and several other leaf morphotypes that appear to belong to Sapindales and potentially Anacardiaceae (Wilf *et al.*, 2005a). An older record, and potentially the oldest macrofossil occurrence worldwide, consists of isolated foliage with characteristic admedially ramified venation from the early Paleocene (early Danian) Salamanca Formation in southern Chubut (Iglesias *et al.*, 2021: morphotype SA050), which was validated in a recent specialist review (Mitchell *et al.*, 2022). The Salamanca Formation has also yielded anacardiaceous pollen, as has the Danian portion of the Lefipán Formation in northwest Chubut (see compilation in Kooyman *et al.*, 2014). Post-Gondwanan Anacardiaceae in the Southern Cone include diverse fossil-wood occurrences (none related to *Dobinea*) from Oligocene to Pleistocene strata of Argentina (*e.g.,* Lutz, 1979; Franco, 2009; Pujana, 2009; reviewed by Pujana, 2022). Additional leaf records attributed to Anacardiaceae come from the ?Paleogene of Chile (Troncoso, 1992) and several Neogene sites in Chile and Argentina (e.g., Troncoso and Encinas 2006; Anzótegui *et al.,* 2007). However, per Burnham and Carranco (2004), additional documentation is needed to confirm some of these occurrences as Anacardiaceae. One notable revision is *Lithraea* *australis* from the Miocene Ñirihuau Formation in Río Negro, Argentina, which Passalia *et al.* (2019) recently transferred from its historical assignment as foliage of the cycad *Zamia* (Berry, 1928).

Paleoecology and biogeography

The diverse Eocene Laguna del Hunco rainforest had multiple strata, from a rich understory with, among many other taxa, ferns, Asteraceae, Solanaceae, and Rubiaceae, to large angiosperm trees of Myrtaceae and Fagaceae and probable coniferous emergents in the Cupressaceae, Araucariaceae, and Podocarpaceae (Gandolfo *et al.*, 2011; Wilf *et al.*, 2014, 2019; Barreda *et al.*, 2020; Deanna *et al.*, 2020; Pujana *et al.*, 2020). The dominance by leaf count of *Dobineaites ameghinoi* suggests high original biomass near the depocenter (*e.g.,* Burnham *et al.*, 1992; Burnham, 1997), comparable to the conifers in the assemblage and *Eucalyptus*, and contrasts sharply with the shrubby or perennial herbaceous habit of extant *Dobinea*, which inhabits more open and seasonally dry environments. These observations indicate that the ancient species had different ecological roles from its living relatives. To the best of our knowledge, there are no published data on *Dobinea* folivore damage for comparison with the fossils. An herbarium survey could be productive for testing the idea of host tracking through time (*e.g.,* Donovan *et al.*, 2023); however, insect mines appear to be very rare on hundreds of *Dobinea* herbarium sheets examined, suggesting that a field study would be necessary.

The proposed affinities of the *D. ameghinoi* fossils to an Asian endemic genus are striking but not surprising because numerous other lineages with extant ranges on the Asian mainland and in maritime Southeast Asia co-occur with *D. ameghinoi* in the same fossil beds at Laguna del Hunco, including *Agathis* (Araucariaceae), *Dacrycarpus* (Podocarpaceae), *Castanopsis* (Fagaceae), *Macaranga* (Euphorbiaceae), and engelhardioid Juglandaceae (Wilf, 2012; Wilf *et al.*, 2014, 2019, 2023; Hermsen & Gandolfo, 2016). Many other Laguna del Hunco genera reach Australasia and Malesia but not the Asian mainland, as summarized elsewhere (*e.g.,* Wilf *et al.*, 2013, 2023; Kooyman *et al.*, 2014). Similarly, Weeks et al. (2014) found from molecular data that long-distance movements characterize the entire evolutionary history of Anacardiaceae. The floristic connections from ancient Patagonia to modern Asia are thought to represent post-Gondwanan lineage survival on the Australian plate (Sahul), followed by exchange with Asia during the Neogene Sahul-Sunda collision (Wilf *et al.*, 2013; Kooyman *et al.*, 2014, 2019; Wilf & Kooyman, 2023). No reliable macrofossils of Laguna del Hunco genera have yet been found in Paleogene (*i.e.,* pre-collision) Asia that would contradict this idea.

CONCLUSIONS

Fossil leaves known since the 1920s as "*Celtis*" *ameghinoi* are the most abundant plant fossils at the extraordinarily diverse Laguna del Hunco locality, early Eocene of Patagonian Argentina. Based on their well-preserved leaf architecture, we could not place these fossils in any previously considered taxa, including the Cannabaceae or any Rosales family. However, we found compelling similarities with the Asian genus *Dobinea* (Anacardiaceae), particularly *D. delavayi*, which is endemic to south-central China. Given its high abundance, *Dobineaites ameghinoi* comb. nov. probably had high biomass, unlike the small-statured living *Dobinea* species, and its diverse insect damage also indicates its paleoecological significance. Our analysis presents a new floristic link from West Gondwana to mainland Asia, as seen in several angiosperm and conifer genera at the same fossil site, and a rare Gondwanan macrofossil record of Anacardiaceae.

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Figure 1. Type specimens of ***Dobineaites ameghinoi*** comb. nov. **1,** Lectotype, USNM 222678 (drawn in Berry, 1925: pl. 3, fig. 1). **2,** Syntype, USNM 222679 (Berry, 1925: pl. 3, fig. 2). **3,** Syntype, USNM 22680 (Berry, 1925: pl. 3, fig. 3). Scale bars: 1 cm.

Figure 2. ***Dobineaites ameghinoi*** comb. nov., selected larger leaves similar to the two syntypes (Fig. 1.2, 1.3). **1-3,** MPEF-Pb 7839, with details of base and margin. Note the pair of thin, obtuse secondary veins emerging near the petiole insertion. **4,** MPEF-Pb 7833. **5,** MPEF-Pb 7857a, with a curvilinear, frass-filled mine (DT90) oviposited adjacent to the midvein (upper arrow), separate oviposition sites on the midvein (DT76, lower arrow), hole feeding (DT2), and margin feeding (DTs 12, 15). Scale bars: 5 cm (1), 1 cm (2–5).

Figure 3. ***Dobineaites ameghinoi*** comb. nov., selected specimens showing general variation with decreasing size and shape, from often larger, broad-cordate forms similar to the two syntypes (Fig. 1.2, 1.3; see also Fig. 2) to smaller, narrow-aspect forms similar to the lectotype (Fig. 1.1). The same variation occurs along single stems in extant *D. delavayi* (Fig. 6.1). Colorization of the leaves results from replacement by secondary minerals. **1,** MPEF-Pb 7778, compressed with an unidentified angiosperm leaf(let) at upper right. **2,** MPEF-Pb 7819. **3,** MPEF-Pb 7763, with numerous galls (DT32), hole feeding (DTs 2, 3), and a pair of thin, obtuse basal secondaries emerging near the petiole insertion (arrow), as found on most of the fossils. **4,** MPEF-Pb 7803, with hole feeding (DTs 1, 3) and skeletonization (DT16). **5,** MPEF-Pb 7890. **6,** MPEF-Pb 7787. **7,** MPEF-Pb 7892 **8,** MPEF-Pb 7754b. **9,** MPEF-Pb 7806. **10,** MPEF-Pb 7797, with a small, probably aborted curvilinear mine oviposited adjacent to the midvein (DT90, arrow). **11,** MPEF-Pb 7829, with margin feeding (DT12). **12,** MJHG 49Pb. **13,** MPEF-Pb 1450, with margin feeding (DT12). Scale bars: 1 cm.

Figure 4. ***Dobineaites ameghinoi*** comb. nov., branch segment with wide-cordate, attached opposite leaves (4.1–4) and selected insect damage (4.5–9). **1,** MPEF-Pb 7901, showing pair of opposite, petiolate leaves. **2,** detail from (4.1) showing pair of small axillary leaves (lower arrows) and a second node with opposite leaf scars (upper arrows) subtending one remaining axillary leaf. **3,** Detail from (4.2, see upper arrows) after preparation, showing the distal leaf node with opposite scars and the remaining axillary leaf, which has marginal teeth and other standard leaf architecture of *D. ameghinoi*, further validating the attached large leaves (1, 2). **4,** Detail from (4.2, see lower arrows) of the paired small, axillary leaves. **5,** MPEF-Pb 7751a, with extensive hole feeding (DTs 1, 2, 3). **6,** MPEF-Pb 7749b, with several serpentine mines preserving sinusoidal, then particulate frass trails (the DT93 exemplar in Labandeira *et al.*, 2007). **7,** detail of one mine in (6), oviposited adjacent to the midvein. **8,** MPEF-Pb 7772, with a wide, possibly aborted mine containing medial particulate frass (the DT91 exemplar in Labandeira *et al.*, 2007). **9,** MPEF-Pb 1053b, with more than 90 oviposition scars (DT54, the scars separately cataloged as MPEF-IC 1370) arrayed in several arcs, previously described as the ichnospecies *Paleovoidus arcuatum* (Sarzetti *et al.*, 2009). Scale bars: 2 cm (1), 5 mm (2), 2 mm (3, 4, 7), 1 cm (5, 6, 8, 9).

Figure 5. Selected cleared leaves representing taxa compared with the fossils (see Discussion) from the Jack A. Wolfe and Leo J. Hickey components of the National Cleared Leaf Collection, housed in the Division of Paleobotany, NMNH, and the Daniel I. Axelrod Cleared Leaf Collection, housed at the University of California Museum of Paleontology, Berkeley. The images are available at https://doi.org/10.25452/figshare.plus.14980698.v1 (Wilf *et al.*, 2021). Names are updated here using World Flora Online. Parentheses denote the

cleared leaf collection (Wolfe, Hickey, or Axelrod), the respective catalog number, and the source herbarium voucher, where applicable. (5.1–5.5), Cannabaceae. **1, *Celtis bungeana*** (Axelrod 162). **2, *Celtis tetrandra*** (Wolfe 9002; A s/n, December 1952, Taiwan). **3, *Aphananthe aspera*** (Wolfe 153; UCH M008603, Panamá). **4, *Trema orientalis*** (Hickey 2834; FM Hueber s/n, Fiji). **5, *Lozanella enantiophylla*** (Wolfe 7036; CAS 422782, Mexico). **6, *Broussonetia kazinoki*** (Moraceae; Hickey 6448; YU, Li Hao-Min 13038, China). **7, *Leucosyke alba*** (Urticaceae; Hickey 6784; YU, Ahern 88, Philippines). **8, *Ampelocera hottlei*** (Ulmaceae; Wolfe 5557; F 1599211, Belize). **9, *Gouania longispicata*** (Rhamnaceae, Wolfe 4863; MO 2053220, Burundi). **10, *Rubus idaeus*** (Rosaceae; Wolfe 1468b; **UCH** 1092750, Alaska). **11, *Rhodotypos scandens*** (Rosaceae; Hickey 3705; US 03703771, Japan). **12, *Croton hircinus*** (Euphorbiaceae; Hickey 6223; US 01229157, Panamá. (5.13–5.15), Malvaceae. **13, *Melochia lupulina*** (Hickey 5555; US 01092271, US Virgin Islands). **14, *Triumfetta columnaris*** (Hickey 5444; US 00535720, Mexico). **15,** *Grewia vitiensis* (Wolfe 11369; UC 1016242, Fiji). **16, *Acer tataricum*** (Sapindaceae; Wolfe 8576; A, Muroi 4232, Japan). **17, *Dobinea delavayi*** (Anacardiaceae; Wolfe 8206**;** A, Rock 6026, Yunnan, China). Scale bars: 1 cm.

Figure 6. Herbarium vouchers of (6.1–6.3) ***Dobinea delavayi*** and (6.4) ***Dobinea vulgaris***. **1,** US 03349094 (Yunnan), showing leaf size and shape variation along a single axis from larger broad-cordate to smaller narrow-lanceolate leaf forms, encompassing much of the variation seen in the fossils (Figs. 1–4), and fertile axes of elm-like fruits. Image courtesy of US via https://collections.nmnh.si.edu/search/botany. **2,** K, G Forrest 15318 (Yunnan), detail of marginal teeth and venation, including thin fimbrial vein (compare, *e.g.,* Fig. 2.3). **3,** P 04860032 (Yunnan), showing wide-cordate leaf morphology and miniature axillary leaves similar to the fossils (Fig. 4.1–4.4). Image courtesy of P via

http://coldb.mnhn.fr/catalognumber/mnhn/p/p04860032. **4,** NY 2592273 (cultivated), showing bases of the opposite elliptical leaves of *D. vulgaris*, with miniature axillary leaf-bearing branches similar to the fossils (Fig. 4.1–4.4). Image courtesy of the C. V. Starr Virtual Herbarium, http://sweetgum.nybg.org/science/vh. Scale bars: 5 cm (1, 3), 1 cm (2, 4).

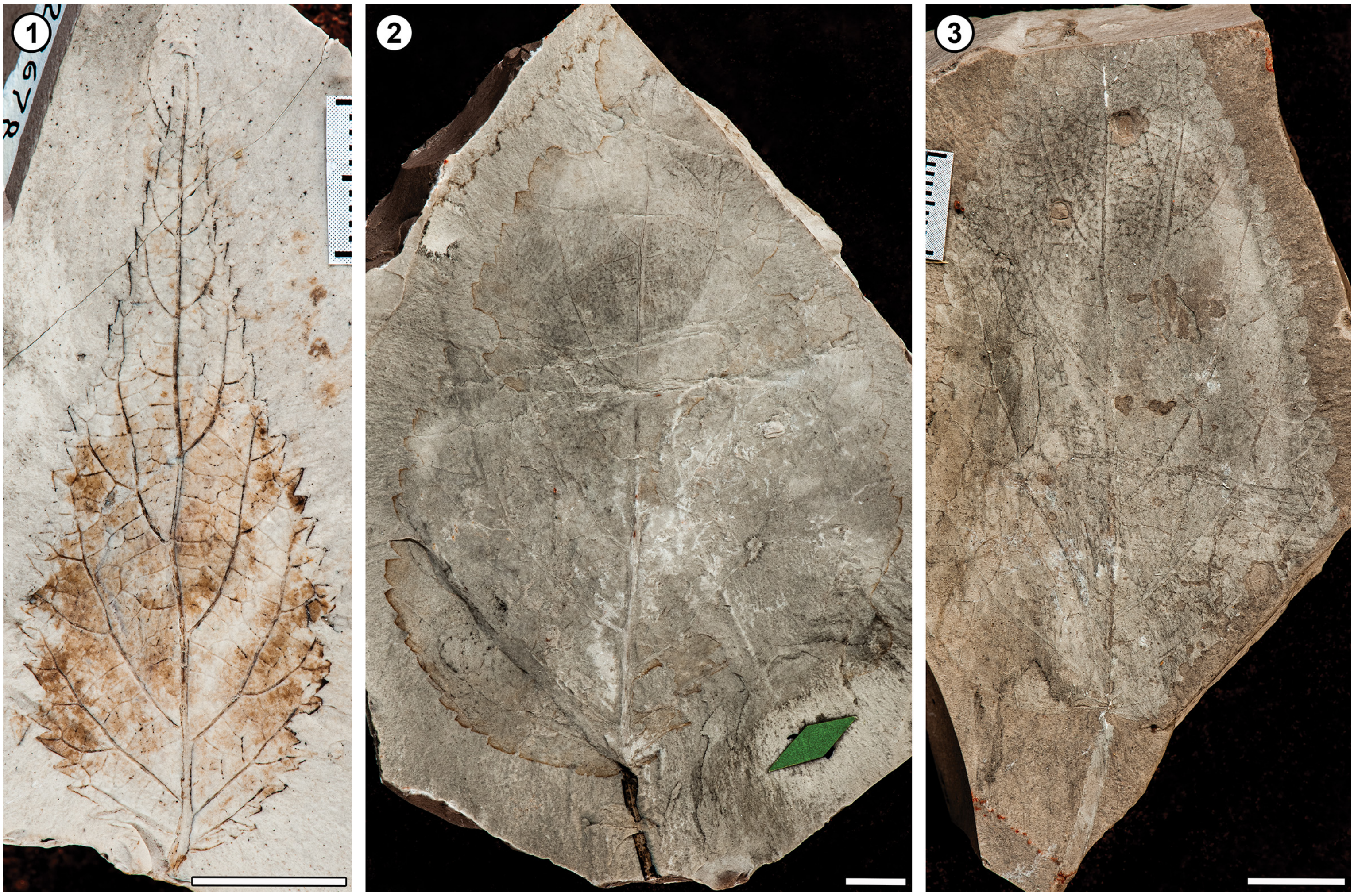


Fig. 1 R1

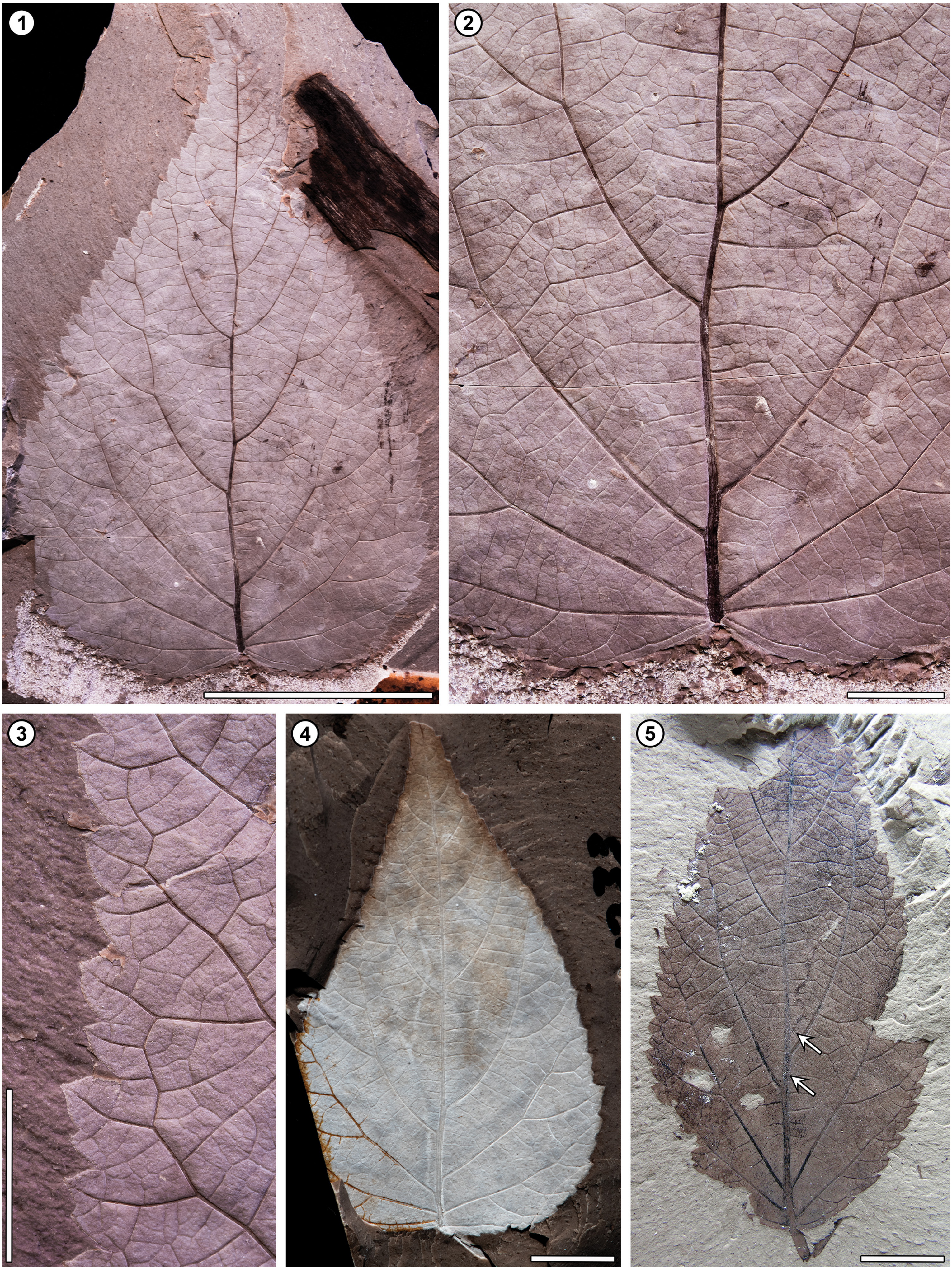
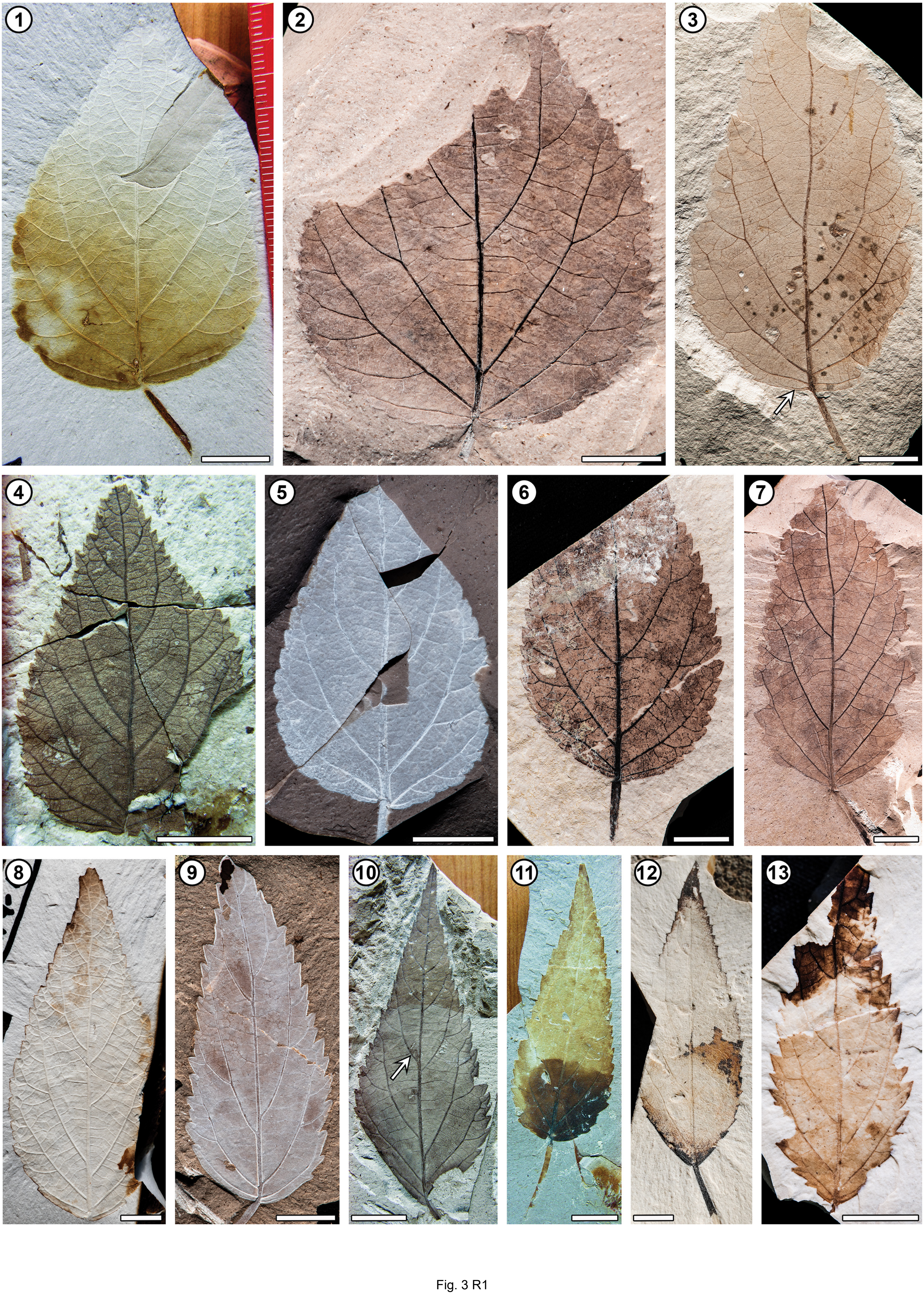


Fig. 2 R1



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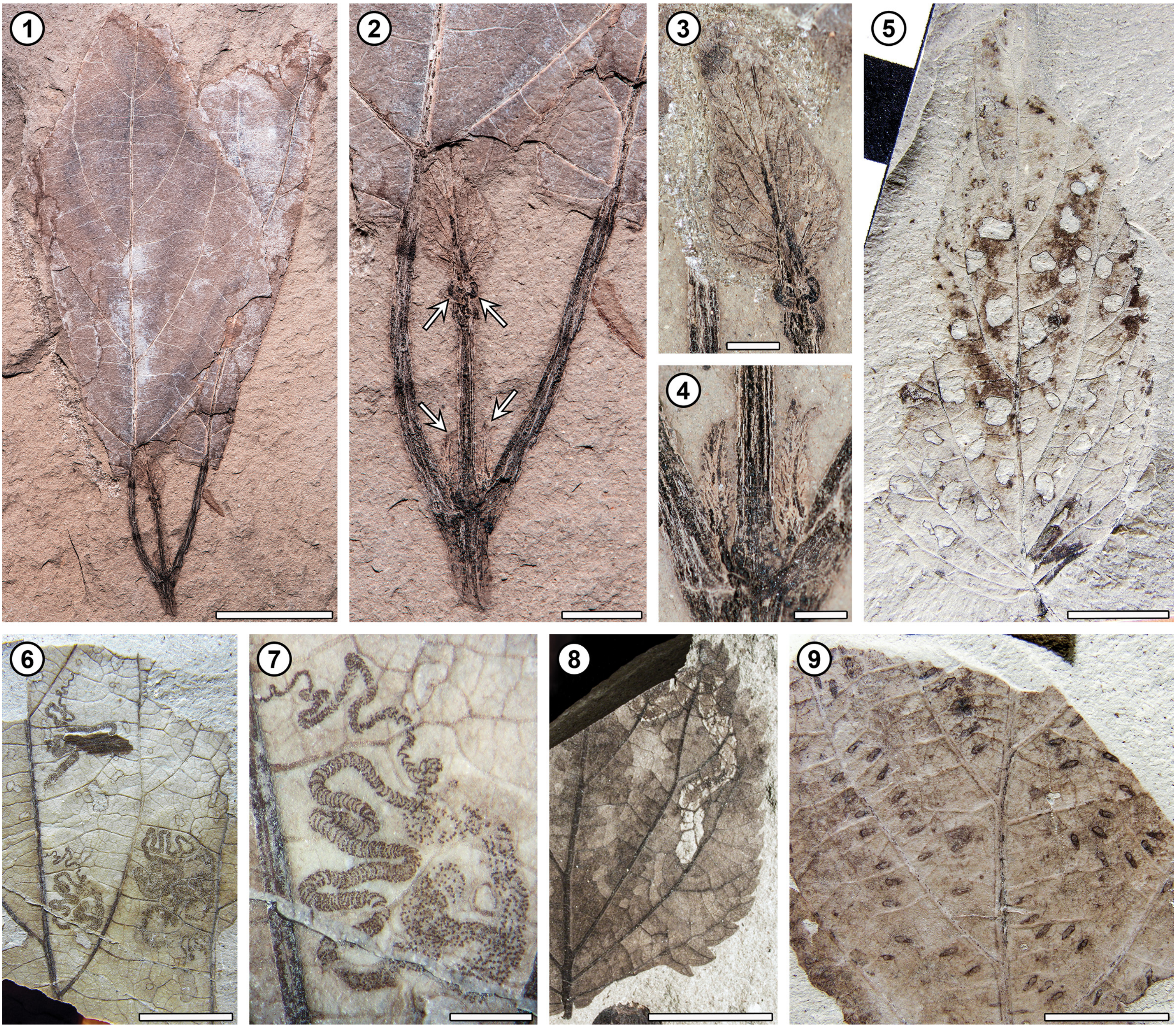

Fig. 4

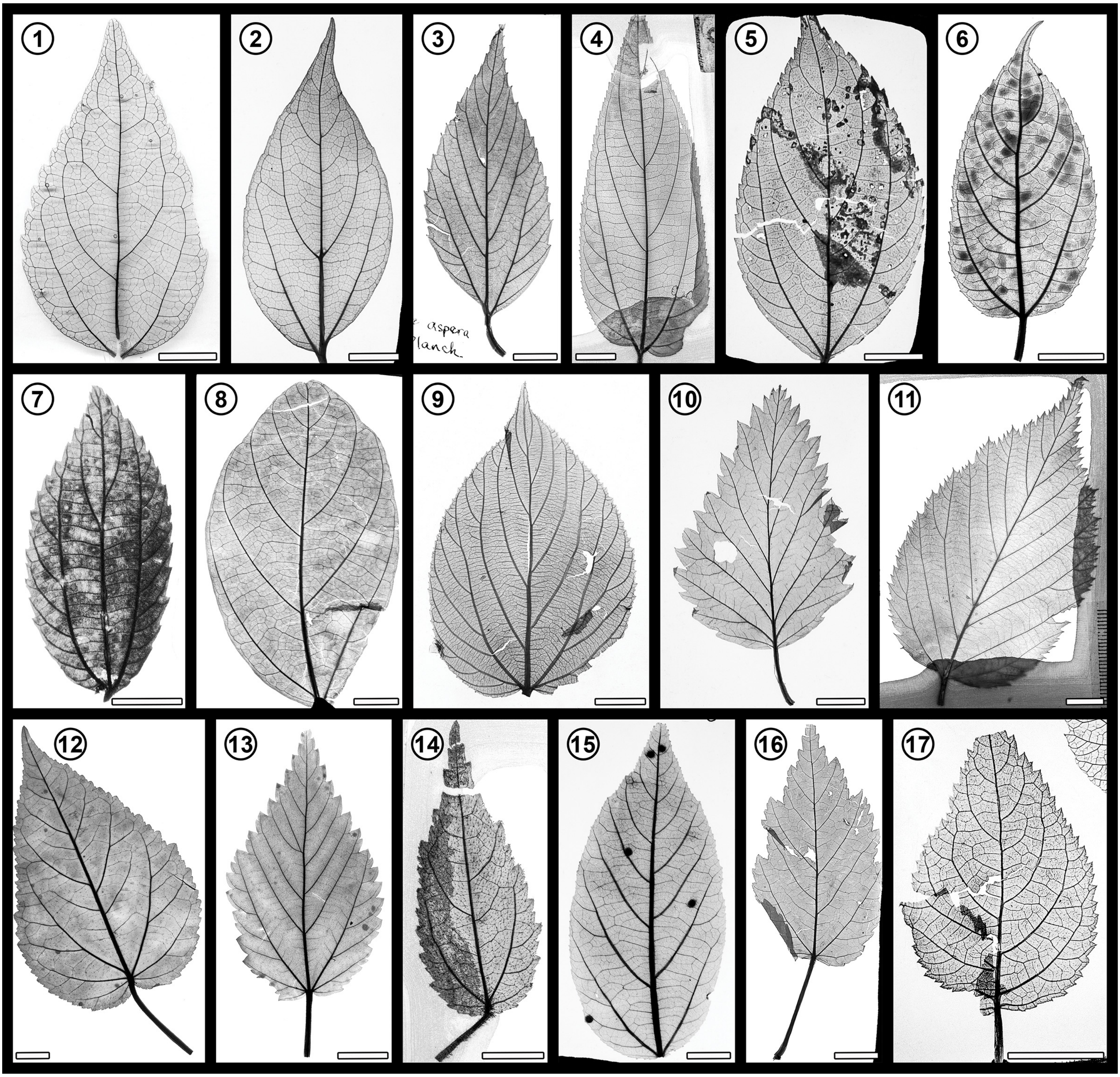

Fig. 5 R1

Fig. 6