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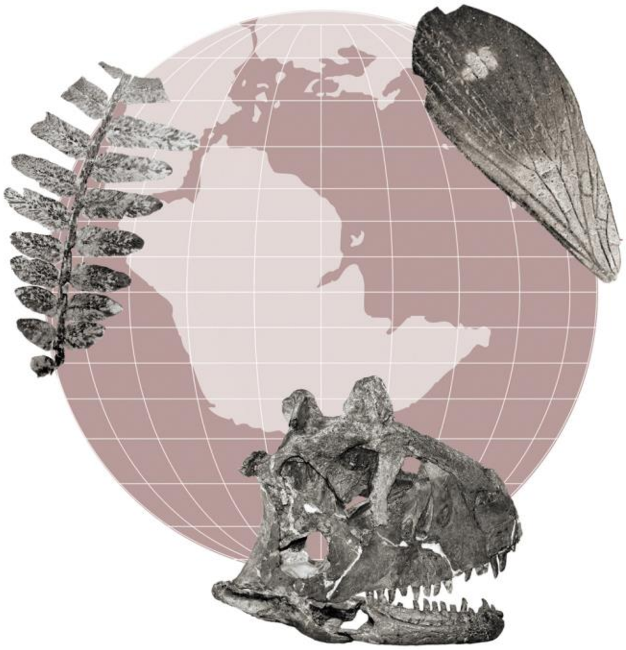

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# A NEW SPECIES OF *MALVACIPHYLLUM* (MALVACEAE: MALVOIDEAE) FROM INLAND PALEOCENE RAINFORESTS OF COLOMBIA

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Short Description: (20 words) A new species of *Malvaciphyllum* sheds light on the diversification of Malvaceae and the early evolution of Neotropical rainforests.

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**Abstract.** Malvoideae, the largest subfamily within Malvaceae, have a distinct fossil record in South America extending back to the Paleocene rainforests of the Cerrejón Fm. in Colombia. We describe *Malvaciphyllum checuorum* sp. nov., a second species of fossil leaf with affinities to Malvoideae, based on leaf impressions from the Paleocene (Selandian) Bogotá Formation in Colombia. Sixty-two leaf impressions of Malvaceae (informal morphotype BF4) were examined. Leaf characters were compared to previously described taxa and affinities to Malvoideae were supported based on the identification of synapomorphic traits of the subfamily. This record is the second species of *Malvaciphyllum* described from the Paleocene of Colombia and likely occupied the most inland *terra firme* conditions of the earliest Neotropical forests.

**Keywords.** Colombia. Neotropics. Leaf. Bogotá Formation. Malvoideae.

**Resumen.** UNA NUEVA ESPECIE DE *MALVACIPHYLLUM* (MALVACEAE: MALVOIDEAE) DE LOS BOSQUES LLUVIOSOS PALEOCENO DEL NORTE DE SURAMÉRICA. Malvoideae, la subfamilia más grande dentro de Malvaceae, tiene un registro fósil distintivo en Sudamérica que se remonta a los bosques lluviosos del Paleoceno de la Formación Cerrejón en Colombia. Describimos *Malvaciphyllum checuorum* sp. nov., una segunda especie de hoja fósil con afinidades a Malvoideae, basada en impresiones de hojas de la Formación Bogotá del Paleoceno medio-tardío en Colombia. Se examinaron sesenta y dos impresiones de hojas de Malvaceae (morfotipo informal BF4). Los caracteres foliares se compararon con fósiles de hojas previamente descritos y se respaldaron las afinidades con Malvoideae basado en la identificación de rasgos sinapomórficos de la subfamilia. Este registro corresponde a la segunda especie de *Malvaciphyllum* descrita del Paleoceno de Colombia, la cual ocurría en zonas de terra firme durante la evolución temprana de bosques Neotropicales.

**Palabras clave.** Colombia. Neotrópico. Hojas. Formación Bogotá. Malvoideae.

MALVACEAE IS A DIVERSE PLANT FAMILY THAT INCLUDES ~4500 SPECIES OF TROPICAL, SUBTROPICAL AND TEMPERATE TREES AND SHRUBS. Recent classification systems include 9–10 subfamilies (Bayer et al., 1999; Colli-Silva et al., 2025) that group the traditionally considered distinct Tilliaceae, Sterculiaceae, Bombacaceae and Malvaceae (s.s.). Within Malvaceae, Malvoideae (formerly Malvaceae s.s.) is the largest group and circumscribes 110 genera and ~1800 species, mainly shrubs. Members of this clade share alternate, simple leaves often bearing stellate hairs, flowers subtended by an epicalyx, monadelphous stamens, and echinate pollen. Although Malvoideae is distributed worldwide, ~75% of its species diversity is centered in the New World (Krapovickas & Fryxell, 2004).

The fossil record of Malvoideae is relatively scarce compared to that of the other recognized subfamilies but includes numerous records of leaves, fruits, pollen, and wood with well-supported natural affinities (see Siegert et al., 2024). The earliest Malvoideae occurrences range back to the late Maastrichtian and consist of pollen of *Malvacipolloides deccanensis* Samant, Mohabey & Dhobale and *M. intertrappea* Samant, Mohabey & Dhobale, as well as fruits of *Harrisocarpon sanhii* Chitaley & Nambudiri and *Daberocarpon gerhardii* Chitaley & Sheikh from the Deccan traps in India (Manchester et al., 2022), indicating the well-established occurrence of Malvoideae in Gondwana by the latest Cretaceous.

In South America, fossil Malvoideae date back to the Selandian (Paleocene) and show a widespread occurrence of leaves, pollen and fruits in the subcontinent throughout the Paleogene. Leaves of *Malvaciphyllum macondicus* M. Carvalho have been described from the Cerrejón Formation in Colombia (Carvalho et al., 2011); a coeval fin-winged fruit, *Aerofructus dillhoffii* Herrera & Manchester, has also been assigned to the Malvaceae (Herrera et al., 2014). Pollen of *Echiperiporites estellae* (Van

Der Hammen & Wymstra) is known from Colombia, Venezuela and Brazil dating back to the Eocene (Jaramillo et al., 2011, Regali et al. 1974a, 1974b; Muller 1981). Paleogene fruits include *Uiher karuen* Siegert, Gandolfo, et Wilf (Siegert et al., 2024) and *Malvacarpus tertiarius* Berry (Berry 1925,) from the early Eocene Laguna del Hunco flora in Patagonia (Wilf et al., 2003), *M. guizañii* Berry (Berry 1938) from the early Eocene Río Pichielufú flora in Patagonia (Wilf et al., 2005), and *M. octoloculus* (Berry 1929) from the early Oligocene Belén flora of Perú (Manchester et al. 2012). Neogene occurrences include leaves of *Malvaciphyllum* from Miocene deposits in Tucumán, Argentina, and Pliocene deposits in Brazil (Anzótegui and Cristalli, 2000). Pollen of *Malvacipolloides maristellae* (Muller, Giacomo & Erve) Da Silva-Caminha, Jaramillo & Absy is common in Miocene deposits of Colombia, Venezuela and Brazil (Hoorn et al., 2019), and Pleistocene wood of *Bastardiopsis* has been previously described from Argentina (Ramos et al., 2017).

Outside of South America, the Cenozoic record of Malvoideae is comparatively sparse. In India, early occurrences of pollen of *Palaeomalvaceaepollis* (*Malvacearumpollis*) Kar date back to the Eocene (Saxena and Trivedi, 2006), whereas other occurrences of the genus date back to the Miocene in Australia, the Indopacific (Hekel, 1972; Khan, 1976) and the Iberian Peninsula (Krutzch, 1966). In Africa, *Echiperiporites* dates back to the Oligocene in Nigeria (Germeraad et al., 1968) and Egypt (El-Beialy, 1990), and additional occurrences have been described from Belgium (Roche and Schüler, 1976). Fruits and other reproductive structures include *Malvocarpon clarus* (Hollick 1928), a fruit from the middle Oligocene San Sebastián Formation in Puerto Rico (Graham 1996) described as resembling *Abutilon*, and Early Miocene flower buds with in-situ pollen of potential Hibiscieae recovered from the Cucaracha Formation in Panamá (Herrera, 2014). Various fossil leaves in North

America have been named under extant genera based on their general resemblance to living taxa, yet their specific natural affinities remain to be fully addressed. These include *Malvastrum exhumatum* Cockerell from the Eocene Florissant Formation (Cockerell, 1907), *Abutilon eakinii* Hollick from Tertiary deposits in Alaska (Hollick et al., 1936), and *Urena miocenica* Graham and *Gossypium arnoldii* Graham, described from the Miocene Trout Creek and Sucker Creek floras in the Columbia River Plateau (Graham, 1963).

In this study, we describe a new species of *Malvaciphyllum* from the Selandian (Paleocene) Bogotá Formation, Colombia. This is the second species of Malvoideae known from the Paleocene of northern South America and contributes to our understanding in the history and diversification of this group on the continent.

**Institutional abbreviations. STRI,** Smithsonian Tropical Research Institute, Panama, Panama; **UR-CP,** Museo de Historia Natural Universidad del Rosario, Bogotá, Colombia.

## MATERIAL AND METHODS

### Geological setting

The examined fossil leaves were collected from the Bogotá Formation, exposed in the Cundinamarca-Boyacá Plateau, Eastern Cordillera of Colombia (Fig. 1.1.). This sedimentary unit is a 1–1.5 km thick sequence of abundant paleosols, massive to laminated mudstones and claystones intercalated with medium to fine-grained sandstones that accumulated in lowland, fluvial environments during the Paleocene and early Eocene, prior to the uplift of the Eastern Cordillera (Morón et al., 2013; Jaramillo et al., 2022). Plant fossils from the Bogotá Formation have been dated as Selandian (Paleocene) in age, based on fossil palynomorph assemblages and biostratigraphic correlation (Carvalho et al., 2021). One of the main stratigraphic and sedimentological differences between the Cerrejón and Bogotá formations lies in the absence of coal deposits in the latter. The Bogotá Formation likely represents more inland *terra firme* conditions, in contrast to the coastal and swampy environments characteristic of the Cerrejón Formation.

## Materials and Methods

The fossil leaf specimens studied herein were collected from five fossil sites found in siltstone and claystone quarries at Tablegrés (Coordinates: 5.066350°, -73.960170°) and Matco (Coordinates: 5.076700°, -73.955300°) brickworks in Cogua Municipality, Cundinamarca, and Checua mine (Coordinates: 5.135725°, -73.846711°) (Fig. 1.1.) in Nemocón Municipality, Cundinamarca, Colombia. We examined 62 complete to partially complete leaf impressions (Morphotype 'BF4' of Carvalho et al. 2021). The specimens were examined under a Nikon SMZ1500 stereoscope and photographed using a Canon 5D DSRL Camera. Leaves were described following the terminology of Ellis et al. (2009) and leaf traits specific to Malvaceae described by Carvalho et al. (2011).

**Figure 1.1.** Collection sites (red stars) for leaves of *Malvaciphyllum checuorum* sp. nov., Cundinamarca, Colombia. Geologic map modified from Gómez et al. (2023).

## SYSTEMATIC PALEONTOLOGY

### Family MALVACEAE Juss.

### Subfamily MALVOIDEAE Burnett

### Genus ***Malvaciphyllum*** Anzótegui

**Type species.** *Malvaciphyllum quenquiadensis* Anzótegui

Upper Miocene of the San José Formation in northwestern Argentina.

***Malvaciphyllum checuorum*** sp. nov. Puente-Santos L.M. & M. Carvalho

Figures 2.1–2.6, 3.1–3.2, 4.1–4.2

**Derivation of name or Etymology.** The epithet *checuorum* refers to the Checua people, a Pre-Columbian population who lived in the area of Nemocón between 6000–500 ybp and who were recently found to be descendants from the earliest populations that spread and differentiated across South America (Krettrek et al., 2025).

**Holotype material.** STRI 12441. Repository Universidad EAFIT, Medellín, Colombia.

**Referred material.** Universidad EAFIT, Medellín: STRI 12078, STRI 12191–12231, STRI 12238, STRI 12239, STRI 12252; Universidad de Caldas, Manizales: STRI 46947, STRI 46950–46952, STRI 46955, STRI 46956, STRI 46974, STRI 46975, STRI 46979–46981, STRI 46990, STRI 46993, STRI 47220.

**Diagnosis.** Leaves ovate, symmetric to laterally asymmetric, dentate to crenulate, petiole double pulvinate. Length to width ratio 3:2. Apex shape straight, base cordate. Primary veins actinodromous, 3–5 basal primary veins; secondary veins craspedrodromous; agrophic veins compound. Secondary and agrophic veins branching proximally and distally. Tertiary veins chevroned percurrent, fourth order veins alternate percurrent. Teeth in two orders, symmetrical, convex-convex, main vein of teeth medial and straight, accessory veins looped.

**Geographic occurrence.** Cogua and Nemocón, Cundinamarca, Colombia (Fig. 1.1).

**Stratigraphic occurrence and age.** Bogotá Formation, Paleocene (Selandian).

**Description.** *Malvaciphyllum checuorum* (Figs. 2.1–2.6, 3.1–3.2, 4.1–4.2) is described based on 62 fossil impressions of complete or nearly complete microphyllous to mesophyllous, toothed leaves. Two fossil specimens show physically associated (attached) leaves of varying size, consistent with the developmental sequence of a shoot apex with alternate phyllotaxy (Figs. 3.1, 3.2). The leaves are petiolate, double pulvinate and marginally attached (Figs. 2.2–2.3); a single complete petiole is 2.4 mm wide at its apex (pulvinus) and 5.1 cm long (Fig. 2.5; STRI 12229). The leaf blades are ovate, unlobed, symmetrical (Fig. 2.6) to medially asymmetrical (Fig. 2.1) and have length:width ratios ranging from 3:2 to 1:1. Leaf apices have a straight shape (Fig. 2.5) and their bases are cordate (Figs. 2.1–2.3).

The leaf primary venation is actinodromous, with 3–5 primary veins that arise from an expanded leaf base (Fig. 2.3). Secondary veins are craspedodromous, excurrent on primary veins, and increasing in spacing proximally. Agrophic veins are compound. Some secondary and agrophic veins can bear 2-3 minor secondaries that branch both proximally and distally close to the margin (Figs. 4.1–4.2). On occasion, minor secondaries from adjacent secondary veins merge together, resembling a semicraspedodromous pattern that is not consistently observed across the whole leaf (Fig. 3.2). Tertiary venation is opposite to alternate percurrent, concentric to the leaf base; costal tertiaries are proximally chevroned and distally sinuous; epimedials are admedially perpendicular to the primary vein and exmedially parallel to intercostal tertiaries. Fourth order veins are alternate percurrent. Areolation is moderate and exterior tertiaries are variable, as they are looped and terminate at the margin (Fig. 4.1, 4.3).

The teeth are regularly spaced, 3 per centimeter, and occur in two discrete orders that differ in size (Fig. 4.3). Larger teeth are usually supplied by secondary and minor secondary veins, whereas the smaller teeth are supplied by tertiary veins. The teeth have angular sinuses and their shape is symmetrical and consistently convex-convex. They exhibit a medial principal vein that terminates at the tooth apex and lacks any type of glandular projection. Accessory veins are present and form a single symmetrical arc that terminates at the tooth apex. A single specimen (STRI 12441) shows a third, larger order of teeth supplied by the first pair of lateral primary veins (Fig. 2.1.).

**Figure 2.1–2.6.** *Malvaciphyllum checuorum* sp. nov. **2.1.** Toothed mesophyll displaying palmate venation pattern. Holotype, STRI 12441. **2.2.** Cordate leaf base and long petiole, STRI 12229. 2.3. Cordate leaf base and petiole with double pulvinus (black arrows), STRI 12209. 2.4. Detail of leaf petiole. Black arrow highlights pulvinus and expanded leaf base, STRI 12229. **2.5.** Leaf apex showcasing straight shape, STRI 12197. **2.6.** Microphyll, STRI 12212. Scale bars = 2 cm.

**Figure 3.1–3.2.** *Malvaciphyllum checuorum* sp. nov. **3.1.** Shoot with five leaves, STRI 12192. **3.2.** Specimen with 3 associated leaves suggestive of alternate phyllotaxy, STRI 12452. Scale bars = 2 cm.

**Figure 4.1–4.3.** Venation details of *Malvaciphyllum checuorum* sp. nov. **4.1.** Detail of proximal (large white arrows) and distal branching (large black arrows) pattern off a secondary vein (large white arrows), STRI 12441. **4.2.** Proximal (large white arrows) and distal (large black arrows) branching of minor secondary veins, STRI 12194. **4.3.** Detail of toothed margin, displaying two orders of teeth size (white arrows), STRI 12193. Scale bars = 1 cm (4.4, 4.2); 2 cm (4.3).

## DISCUSSION

### Natural affinities

In this study we describe a new species of *Malvaciphyllum* from the Paleocene Bogotá Fm. in central Colombia. This form-genus was originally proposed by Anzótegui and Cristalli (2000) to describe leaves of Malvaceae (sensu stricto) from the Miocene San José Fm in Tucumán, Argentina, and Pliocene deposits in the State of Maranhao, Brazil. Traits observed in these fossil species, namely the distally and proximally branching secondary veins, were found to be synapomorphic to Malvoideae, based on a family-wide study on leaf architectural traits (Carvalho et al., 2011).

*Malvaciphyllum checuorum* resembles leaves of Malvaceae in having a cordate shape, crenulate margin, palmate venation and pulvinus —, traits common within this family (Gentry, 1993; Stevens, 2001). Numerous leaf fossils have been previously described as either morphotaxa or assigned to extant genera within Malvaceae (see Carvalho et al., 2011 for a morphological comparison of fossil leaves of Malvaceae. Additional reported taxa include Anberré et al., 2015; Xu et al., 2020; Hazra et al., 2022; Nishino et al., 2023; Yamada et al., 2025). All of these taxa share having a palmate venation, cordate base, percurrent tertiary veins, a pulvinus, and crenate margin (sometimes entire; Hazra et al., 2022) with malvoid teeth. Among these taxa, only *Malvaciphyllum* exhibits the proximal and distal branching pattern of secondary veins that identifies leaves of Malvoideae (Carvalho et al., 2011). This trait is also present in leaves of *Malvaciphyllum checuorum* and supports their description within the genus.

Leaves of *Malvaciphyllum checuorum* however differ from previously described species of *Malvaciphyllum*. The prominent rounded lobes and opposite-percurrent tertiary venation of *M. quenquiadensis* (Miocene, Tucumán, Argentina; Anzótegui and Cristalli, 2000) consistently differs from the unlobed shape and chevroned tertiary venation of *M. checuorum*, supporting species delimitation. Similarly, *M. checuorum* also differs from coetaneous *M. macondicus* in their size, shape, teeth morphology.

Whereas *M. macondicus* includes (mostly) mesophyllous leaves with 1:1 length–width ratios and 2-3 orders of teeth, leaves of M. *checuorum* are smaller, mainly notophylls and microphylls, they exhibit length–width ratios of 3:2, and have 1-2 orders of teeth. The relative size of teeth also differs across both species: whereas *M. macondicus* has ~5 teeth per cm, each one supplied by accessory veins that loop into a series of arches (Carvalho et al., 2011), *M. checuorum* has larger teeth, only ~3 per cm, each one supplied by accessory veins that form a single arc. These distinctions support species delimitation between *M. macondicus* from the Paleocene Cerrejón Fm. in northern Colombia and *M. checuorum* from the Paleocene Bogotá Fm. in Central Colombia.

## Paleocene malvoids in northern South America

Paleocene floras in northern South America depict early stages in the evolution of modern-like Neotropical rainforests. The end-Cretaceous extinction event had pervasive effects on the region, triggering the extinction of ~45% of plant species, which was followed by a slow recovery of species diversity that lasted ~6–8 million years. The open-canopy, mixed forests of the Maastrichtian were replaced by closed-canopy, angiosperm-dominated forests that resemble the modern family-level composition observed in Neotropical rainforests today (Carvalho et al., 2021). The Paleocene floras of the Bogotá and Cerrejón Formations depict local plant communities in the Sabana de Bogotá and Ranchería Basins, respectively, that illustrate this pattern, sharing a similar family-level composition that includes abundant aquatic and terrestrial ferns (Wing et al., 2009: *Salvinia*), potential canopy elements such as Fabaceae (Herrera et al., 2019), Lauraceae, Annonaceae, Euphorbiaceae, Ulmaceae (Herrera et al., 2014); monocots include Arecaceae (Gomez et al., 2009) and aroids (Herrera et al., 2008) and multiples families with climbing habits, such as Menispermaceae (Doria et al., 2008; Herrera et al., 2011), Vitaceae (Herrera et al., 2024), Icacinaceae (Stull et al. 2012), and Passifloraceae.

The occurrence of two different species of *Malvaciphyllum* from the Bogotá and Cerrejón Formations highlights taxonomic differences between both floras at the sub-familial level that are consistent with observed ecological and environmental differences in both sedimentary units. Whereas the coal-rich deposits of the Cerrejón Formation depict a transition from coastal deltaic systems to peat-accumulating floodplains and swamps, the Bogotá Formation is a meandering to anastomosing fluvial system that accumulated in an inland depositional system. The peat-accumulating environments of Cerrejón contrast with the thick, highly weathered paleosol sequences of the Bogotá Formation, which are suggestive of well-drained environments. These environmental distinctions match physiognomic, functional, and ecological differences between both floras: whereas leaf size in the Cerrejón flora is generally larger and provides mean annual precipitation estimates of >250 cm of annual rainfall, leaves from the Bogotá flora provide estimates of ~180 cm MAP (Carvalho et al., 2021). Leaf mass per area, a functional trait that relates to various climatic and environmental parameters (Butrim et al., 2024), also differs between both floras: whereas leaf morphotypes from the Bogotá Flora have an average value of 128.39 g/m$^2$, those from the Cerrejón Flora show an average value of 92.49 g/m$^2$ (Giraldo et al., 2021). The Bogotá Flora is characterized by having a diverse assemblage of insect-feeding interactions that exceeds in richness those observed in any other Paleocene flora described to date (Giraldo et al., 2021). In contrast, plant-insect interactions in the Cerrejón flora are relatively depauperate. Whereas leaves in the Bogotá Flora show ~60 distinct insect-feeding damage types (rarefied to 400 leaves), leaves from the Cerrejón Flora only have ~25 (rarefied to 400 leaves) (Giraldo et al., 2021).Given the small number of complete leaves (nearly complete blades that include a petiole) recovered for M. checuorum and M. macondicus, it was not possible to quantify and evaluate differences in their leaf mass per area. Nonetheless, their size follows the general trends observed between both floras. Whereas *M. checuorum* includes microphylls, notophylls and mesophylls, leaves of *M. macondicum* are generally larger (microphylls, notophylls, mesophylls and macrophylls). This distinction is consistent with lower precipitation and/or a more marked water stress regime in the well-drained environments at Bogotá than in the peat-accumulating environments of the Cerrejón Formation. Ecological and environmental differences in the Sabana de Bogotá and Ranchería Basins may have created distinct selective pressures and ecological opportunities that enabled the radiation of tropical plant taxa in the aftermath of the end-Cretaceous extinction. This idea is consistent with an inferred increase in diversification rates of tropical plant families after the end-Cretaceous extinction event (Ramírez-Barahona et al., 2020). Even though Paleocene Malvaceae from northern South America also includes pollen (*Bombacacidites* spp.; Carvalho et al., 2011) and fruits (*Aerofructus dillhoffii*; Herrera et al., 2014), none of these were found in organic connection and therefore cannot be associated to the same biological taxon. Natural affinities of both *Bombacacidites* spp. and *A. dillhoffii* are suggestive of Bombacoideae, providing evidence of the occurrence of other lineages of Malvaceae in these floras. The fossil genus *Malvaciphyllum* bears synapomorphic traits that support an affinity to Malvoidae, but does not necessarily represent a single lineage within the clade. The occurrence of two different species of *Malvaciphyllum* in the Paleocene Bogotá and Cerrejón floras in northern South America indicates the widespread occurrence of Malvoideae and their diversification in the early evolution of Neotropical rainforests.

## CONCLUSIONS

*Malvaciphyllum checuorum* is a new species of Malvoidae from the Paleocene Bogotá Formation of Colombia. – the second to be described from Paleocene Neotropical rainforests of northwestern South America. This new taxon differs from previously described and coeval *M. macondicus* from the Cerrejón Formation in leaf size, tooth size and frequency. The distinction of a new species of Malvoideae in the Paleocene rainforests of northwestern South America contributes the relatively sparse fossil record of the group and is consistent with their diversification following the end-Cretaceous extinction.

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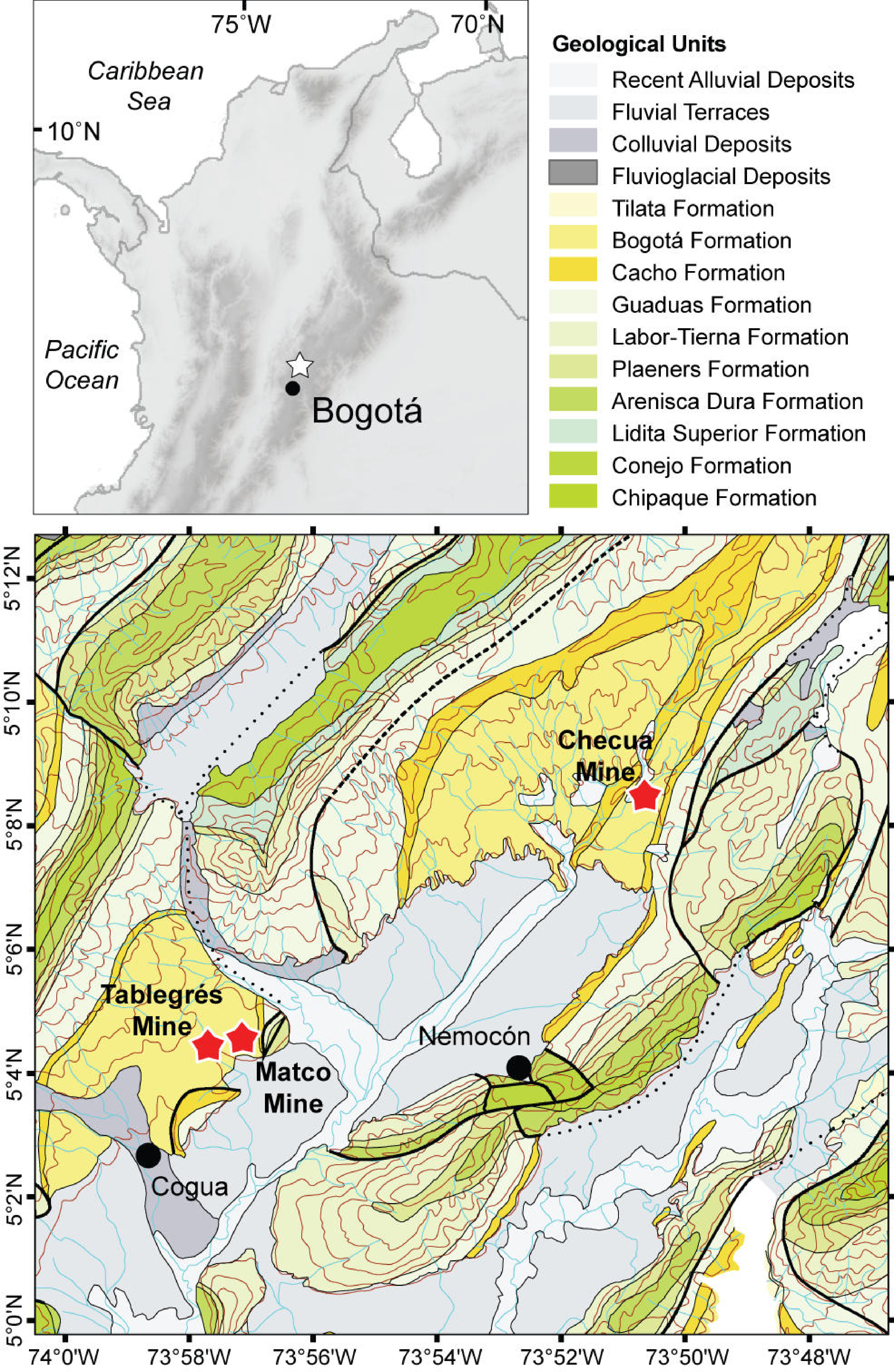
75°W
70°N
Caribbean Sea
10°N
Pacific Ocean
Bogotá
Geological Units
Recent Alluvial Deposits
Fluvial Terraces
Colluvial Deposits
Fluvioglacial Deposits
Tilata Formation
Bogotá Formation
Cacho Formation
Guaduas Formation
Labor-Tierna Formation
Plaeners Formation
Arenisca Dura Formation
Lidita Superior Formation
Conejo Formation
Chipaque Formation
5°12'N
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5°6'N
5°4'N
5°2'N
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Checua Mine
Tablegrés Mine
Matco Mine
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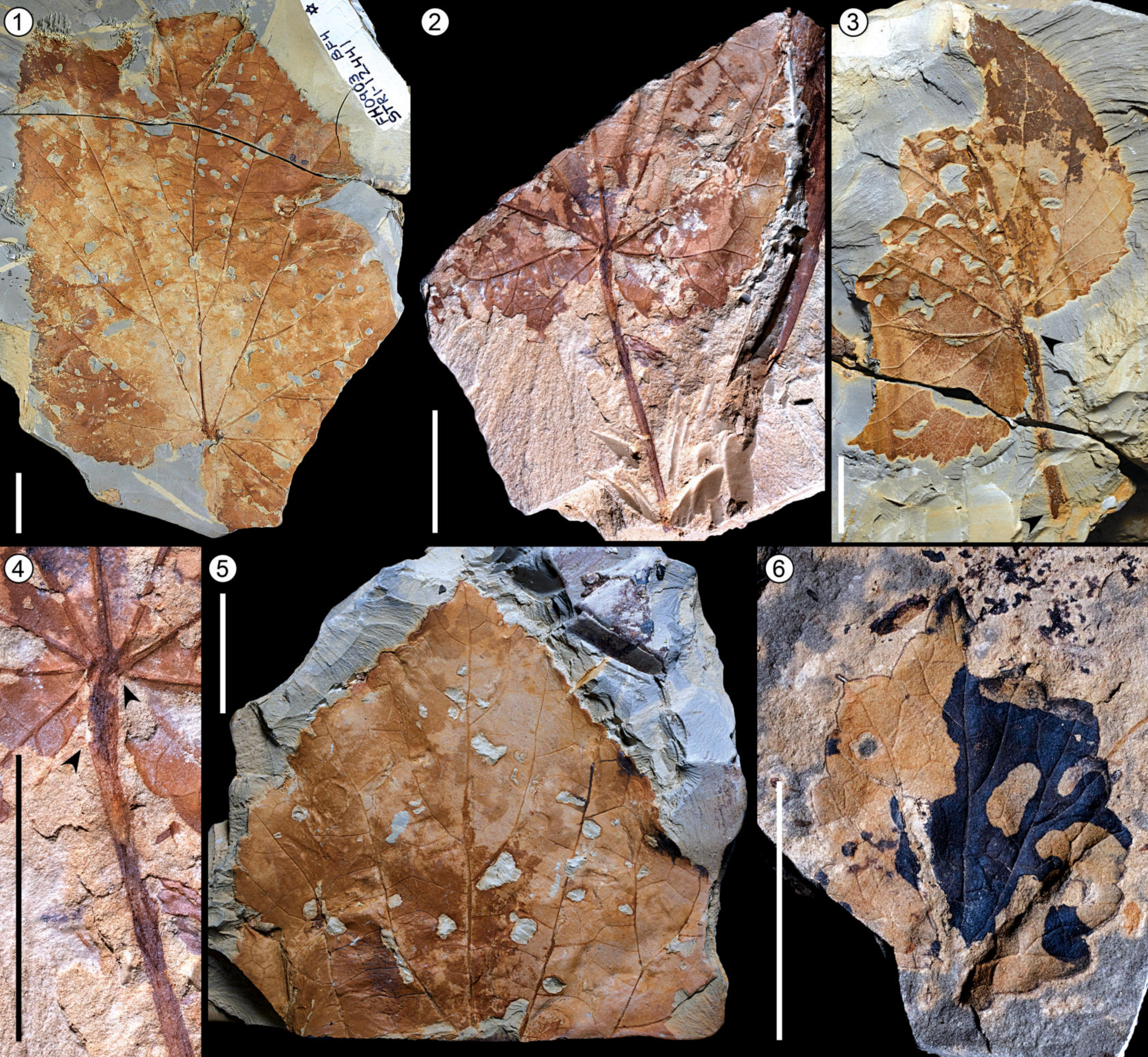
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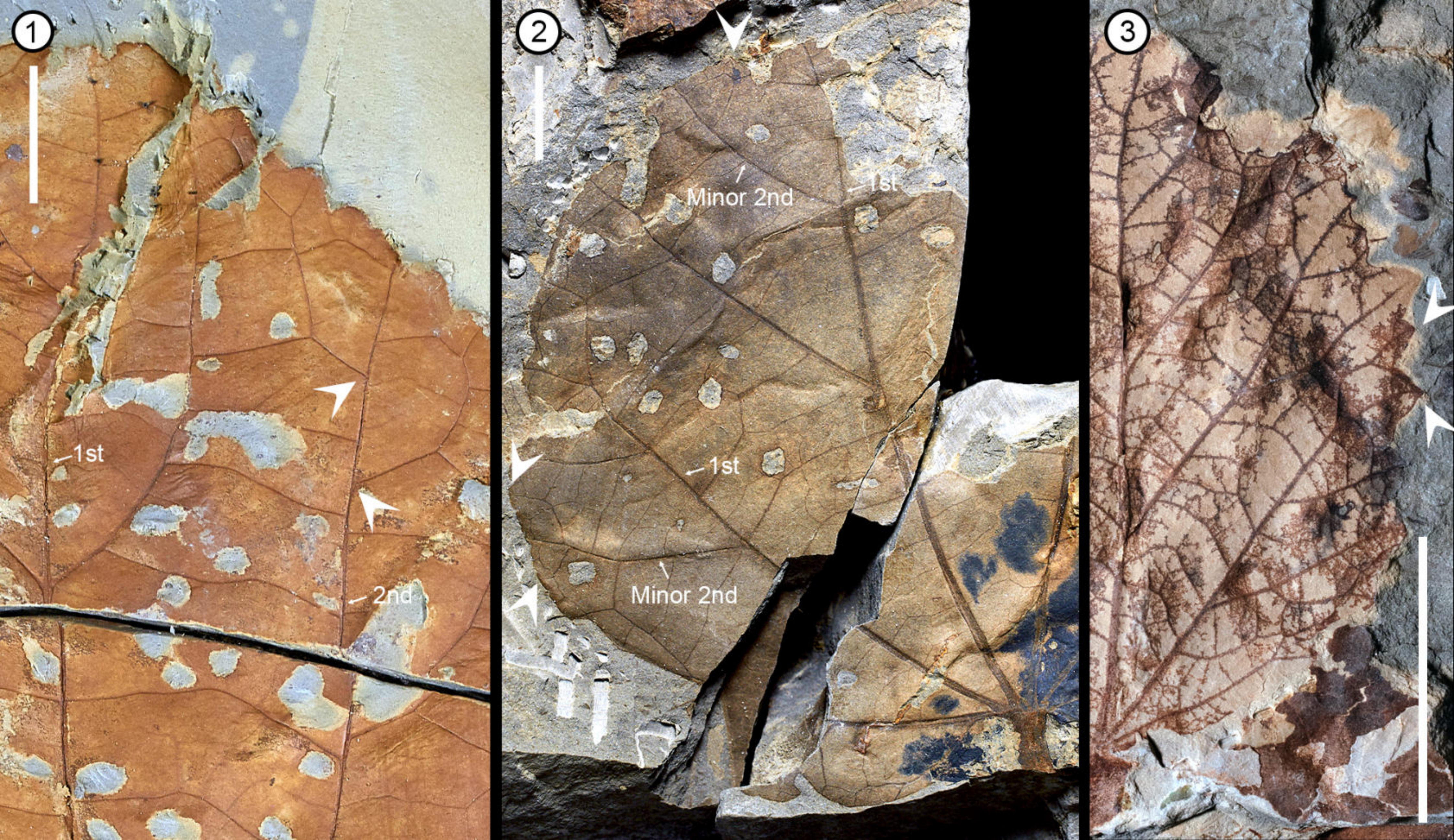
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