

EARLY RECORDS OF MELASTOMATACEAE FROM THE MIDDLE–LATE PALEOCENE RAIN FORESTS OF SOUTH AMERICA CONFLICT WITH LAURASIAN ORIGINS

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Editor: Kathleen B. Pigg

Premise of research. Melastomataceae are a diverse and primarily tropical family with a particularly sparse fossil record. Various biogeographic interpretations based on phylogenies, extant distribution, and a limited fossil record have placed the origin of the family in either Laurasia or Gondwana (eastern or western).

Methodology. We describe *Xystonia simonae* M. Carvalho gen. et sp. nov. on the basis of fossil leaves from middle–late Paleocene deposits of the Bogotá Formation in central Colombia. These leaves have a characteristic acrodromous venation pattern common among subfamily Melastomatoideae. The leaves are compared with various acrodromously veined fossils and living angiosperms to assess their natural affinities.

Pivotal results. The fossil leaves described predate the earliest known occurrence of Melastomatoideae by 5–7 Myr and conflict with previous interpretations that considered Melastomatoideae as Laurasian in origin. In revising the fossil record of Melastomataceae, we reevaluated the age of *Melastomaephyllum danielis* Huert. to be Miocene (previously Eocene/Oligocene) using pollen obtained from the rock that contained the type specimen.

Conclusions. Our findings contribute to the scant early records of Melastomataceae and show that Melastomatoideae was part of a tropical rain forest assemblage by the middle–late Paleocene. Leaf galls and other leaf damage on *X. simonae* evidence intense and specialized biotic interactions in the early evolution of this lineage.

Keywords: leaves, paleobotany, Bogotá Formation, *Xystonia*, *Melastomaceophyllum*.

Online enhancement: supplemental figure.

Introduction

Melastomataceae (including Memecylaceae; APG 2009) are a diverse family of mostly tropical trees and shrubs as well as lianas, herbs, and epiphytes. They include over 5000 species in ca. 165 genera (Christenhusz and Byng 2016), only two of which occur naturally in subtropical and temperate areas (i.e., *Miconia* sect. *Miconiastrum* (Bonpl. ex Naudin) Judd, Bécquer, & Majure and *Rhexia* L., respectively). The diversity of the family is centered in the Neotropics, where ~3500 species occur among a wide variety of habitats, including lowland tropical rain forests, savannas, cerrados, montane cloud forests, paramos, and punas (Michelangeli et al. 2013; Veranso-Libalah et al. 2018).

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Despite their extant diversity, Melastomataceae have a particularly scarce fossil record. Pollen morphology is similar among families of Myrtales (Muller 1981; Patel et al. 1984), and it is therefore difficult to confidently differentiate Melastomataceae from other Myrtalean taxa in the palynological sedimentary record (Morley and Dick 2003). Therefore, confident occurrences of Melastomataceae have mostly relied on macrofossils. Early records of the family have been considered to be “centered in Laurasia” (Renner et al. 2001) and include *Acrovena laevis* Hickey from the early Eocene Golden Valley Formation (Hickey 1977) and other acrodromously veined leaves from the Eocene Republic flora of the Klondike Mountain Formation in North America (Wehr and Hopkins 1994); *Tibouchina*-like leaves from the Eocene/Oligocene deposits of the Fonseca Formation in Brazil, previously considered to be Late Miocene/Pliocene (Duarte 1956; Maizatto et al. 2008); and Eocene/Oligocene wood of Olisbeoideae from Germany (Gottwald 1992). It is worth noting that Melastomataceae-like leaves from the Eocene Klondike Mountain Formation (Wehr and Hopkins 1994) are currently under study and appear to be of uncertain affinity

(K. Pigg, personal communication). Miocene and Pliocene occurrences are more widespread and include leaves and seeds in Eurasia (Collinson and Pingen 1982), North America, Ecuador and Bolivia (cited in Renner 2004a), Borneo (*Melastomaceophyllum* sp., age revisited from Eocene to Miocene; Geyler 1887; Kräusel 1929), and Sumatra (*Melastomaceophyllum geylei* Kräusel; Kräusel 1929). From Colombia, *Melastomaceophyllum danielis* was previously considered of Eocene or Oligocene age (see below; Huertas 1977). Additional records of leaves and reproductive structures described under *Melastomites* Unger are fragmentary, and their affinity to Melastomataceae remain unconfirmed (see table 1).

Tribal delimitations and phylogenetic relationships within the family have been in continuous revision over the past ca. 30 yr (e.g., Renner 1993; Clausing and Renner 2001; Penneys et al. 2010; Michelangeli et al. 2011; Da Rocha et al. 2018; Bacci et al. 2019; Bochorny et al. 2019; Penneys et al. 2020). Although the position of some basal lineages may be unclear (i.e., *Pternandra* Jack), two main groups are currently recognized within the family (Penneys et al. 2020): Olisbeoideae (former Memecylaceae) and Melastomatoideae, currently grouped into 18 tribes that all share opposite leaves with acrodromous venation (Clausing and Renner 2001), although some exceptions exist. Some lineages have secondarily lost their acrodromous condition (e.g.,

Table 1
Morphological Distinctions between *Xystonia simonae* sp. nov. and Previously Described Leaves of *Melastomites* Unger and Melastomataceae Juss.

| Taxon | Age | Location | Morphological differences with <i>X. simonae</i> | Reference(s) |
|---|------------------|--------------------|---|--|
| <i>Melastomites montanensis</i> Brown | Paleocene | United States | Long petiole, horizontal (opposite percurrent?) tertiaries; affinity to Melastomataceae was dismissed by Renner et al. (2001) and Manchester (2014) | Brown 1962 |
| <i>Acrovena laevis</i> Hickey | Eocene | United States | Various pairs of secondary veins | Hickey 1977 |
| Unnamed leaves from Klondike Mountain Formation | Eocene | United States | Various pairs of secondary veins; affinity uncertain | Wehr and Hopkins 1994; Renner et al. 2001 |
| <i>Melastomites americanus</i> Berry | Eocene | United States | One pair of basal secondaries and various secondary veins along the midrib | Berry 1916 |
| <i>Melastomites ovatus</i> Berry | Eocene | United States | Pseudoacrodromous venation with four basal veins and three accessory secondaries along the midvein; leaf asymmetrical | Berry 1930 |
| <i>Melastomites verus</i> (Berry) Berry | Eocene | United States | Various pairs of secondary veins | Berry 1930 |
| <i>Melastomaceophyllum</i> sp. | Eocene | Borneo | Tertiaries straight percurrent | Geyler 1887; Kräusel 1929 |
| <i>Melastomites quinquenervis</i> Heer | Eocene | Switzerland | Toothed margin, five basal veins | Heer 1855 |
| <i>Tibouchina dolianitii</i> Duarte | Eocene/Oligocene | Brazil | Various pairs of secondary veins | Duarte 1956 |
| <i>Tibouchina santosii</i> Duarte | Eocene/Oligocene | Brazil | Various pairs of secondary veins | Duarte 1956 |
| <i>Melastomites druoidum</i> Unger | Eocene/Oligocene | Slovenia | Toothed margin | Unger 1850 |
| <i>Melastomites cuneiformis</i> Hosius et von der Mark | Oligocene | Germany | Leaf fragment; tertiaries straight percurrent | Hosius and von der Mark 1880 |
| <i>Melastomites dominguensis</i> Berry | “Tertiary” | Dominican Republic | Fragment; tertiaries resemble <i>X. simonae</i> ; no apex or base | Berry 1921 |
| <i>Melastomites angustus</i> Berry | Miocene | Mexico | Tertiaries strongly straight percurrent and exterior tertiaries acute to midvein | Berry 1923 |
| <i>Melastomites obovatus</i> Berry | Miocene | Mexico | Straight percurrent tertiaries | Berry 1923 |
| <i>Melastomaceophyllum</i> <i>danieli</i> Huert. | Miocene | Colombia | Tertiaries strongly straight percurrent | Huertas 1977 |
| <i>Melastomaceophyllum</i> <i>geylei</i> Kräusel | Miocene | Sumatra | Tertiaries strongly straight percurrent | Kräusel 1929 |
| <i>Melastomites incertus</i> Berry ex LaMotte | Miocene | Panama | Tertiaries strongly straight percurrent | Berry 1918; LaMotte 1952 |
| <i>Melastomites trinervia</i> Unger | Miocene | Croatia | Toothed margin | Unger 1869 |
| <i>Melastomites miconioides</i> Weber | Miocene | Germany | Venation pseudoacrodromous/distally brochidodromous | Weber 1852 |
| <i>Melastomites lanceolata</i> Weber | Miocene | Germany | Small, linear leaves with length-to-width ratio >4 | Weber 1852 |
| <i>Melastomites</i> <i>marumiaefolius</i> Weber | Miocene | Germany | Looping exterior tertiaries | Weber 1852 |
| <i>Melastomites menzelii</i> Weyland | Miocene | Germany | Two pairs of basal major veins, distally looping exterior tertiary veins | Weyland 1934 |

Alloneuron Pilg.; Wallnöfer 1996), and the evolution of extreme anisophylly/abortion of one leaf per pair has resulted in alternate leaves (e.g., *Phainantha* spp.; Ulloa and Neill 2006). Species relationships at the tribal level have revealed a complex biogeographic history in which long-distance dispersals played a major role. Numerous dispersal events throughout the Cenozoic likely explain the current distribution of the family in Asia, Africa, Madagascar, and the Caribbean, as relatively derived taxa occurring in these regions are nested within continental Neotropical clades/grades (Renner and Meyer 2001; Renner 2004b; Michelangeli et al. 2008; Veranso-Libalah et al. 2018; Wurdack and Michelangeli 2019).

Inferences of ancestral areas and the early evolution of Melastomataceae remain nonetheless contentious for the following reasons: (1) a limited yet Laurasian-centered fossil record contrasts with the mainly pantropical distribution of the family, (2) divergence and diversification age estimates based on molecular clock approaches can vary widely owing to the small number of fossil calibrations available (compare Renner et al. 2001; Renner and Meyer 2001; Morley and Dick 2003; Renner 2004a, 2004b), and (3) ancestral area reconstructions based on phylogenies have shown to be susceptible to taxon sampling and the position of major clades within the family tree (compare Renner 1993; Berger et al. 2016; Veranso-Libalah et al. 2018). Various biogeographical hypotheses based on the phylogeny, extant distribution, and limited fossil record of Melastomataceae have been proposed in relation to the origin and early evolution of the family (Renner et al. 2001; Morley and Dick 2003; Renner 2004a, 2004b; Sytsma et al. 2004; Berger et al. 2016; Veranso-Libalah et al. 2018). Using divergence age estimations and their earliest known fossils, Renner et al. (2001) suggested a Laurasian origin for the family, whereas biogeographic interpretations based on extant distribution and phylogenies place the origin of Melastomataceae in eastern (Renner 1993) or western (Raven and Axelrod 1974; Gentry 1982, 1993; Jacques-Félix 1994) Gondwana. Only a thoroughly sampled fossil record can fully support or falsify any of these hypotheses.

Here, we describe leaves of Melastomatoideae from the middle–late Paleocene (58–60 Ma) rain forests of the Bogotá Formation in central Colombia. These fossils predate the earliest known record of the family by 5–7 Myr and contribute to the poor early record of the family. The new fossils also indicate that middle–late Paleocene Melastomatoideae grew in northern South American rain forests, rejecting an early Eocene Laurasian origin for this lineage (Renner et al. 2001).

Material and Methods

Geological Setting

The Bogotá Formation is a 1.6-km-thick depositional sequence composed of extensive thick siltstones, clay stones, paleosols, interbedded sandstones, and sporadic conglomerates and breccias that outcrop along the Eastern Cordillera in central Colombia. These deposits accumulated throughout the middle–late Paleocene and early Eocene in fluvial lowland environments that predate the Andean uplift in northern South America and include laterally meandering channels and floodplains with abundant paleosol development (Bayona et al. 2008, 2010).

A diverse array of plant and vertebrate fossils are known from the Bogotá Formation, including xenungulate mammals (Villaroel 1987), marsupials, mesoeucrocodylians, anurans, dipnoan fishes (Bloch et al. 2008), turtles (Cadena 2014), and squamates such as iguanians and snakes (Head et al. 2012). Pollen assemblages retrieved from fossiliferous sites of the Bogotá Formation belong to the T-03B *Foveotricolpites perforates* zone of Jaramillo et al. (2011), indicating a middle to late Paleocene age (ca. 58–60 Ma). Volcanic zircons collected from the type section of the Bogotá Formation yield have shown a Late Paleocene age of 56.2 ± 1.6 Ma according to LA-ICP-MS $^{206}\text{Pb}/^{238}\text{U}$ analyses (Bayona et al. 2010).

Fossil Locality

We collected 24 leaf fossils from a single fossiliferous bed exposed at the Parque Minero Industrial el Mochuelo in central Colombia (fig. 1; lat. 4.5336°N, long. 74.1399°W). Maximum depositional ages based on $^{206}\text{Pb}/^{238}\text{U}$ of detrital zircons from the type section of the Bogotá Formation show a distinct onset of volcanism throughout the middle Paleocene and early Eocene (Bayona et al. 2010). Detrital zircons from fluvial sandstones directly above and below fossil locality 860015 lack the distinct late Paleocene volcanic signal seen elsewhere, therefore providing a minimum age of 58 Ma for the fossil leaves and a maximum age of 60 Ma, corresponding to the oldest estimate for the Bogotá Formation.

Fossil Imaging and Repository

Fossils were informally grouped into leaf morphotype BF84 according to shape and venation characters using the terminology of Ellis et al. (2009). Leaf damage was identified using Labandeira et al. (2007). All specimens were photographed with a Canon EOS 5DS R, and reversible image adjustments, such as white balance, temperature, and contrast, were made using Adobe Photoshop CC 2018. Leaf fragments were scanned using an environmental scanning electron microscope (Zeiss Evo 40 BP). Measurements were taken using ImageJ (Schneider et al. 2012). The leaf fossils are stored in the paleontological collections of the Museo Mapuka at Universidad del Norte, Barranquilla, Colombia. Additional information on the fossil material can be obtained through the Smithsonian Tropical Research Institute Geology Database (<https://biogeodb.stri.si.edu/jaramillosdb/web/>).

Comparative Material

Leaf fossils were compared with angiosperm lineages that have leaves with acrodromous venation using the National Cleared Leaf Collection stored at the Smithsonian Natural History Museum (USNM), botanical collections at the Joaquín Antonio Uribe Herbarium (JAUM) in Medellín, Colombia, and at the US National Herbarium (US). The leaf fossils were also compared with leaf taxa previously described and associated to Melastomataceae using descriptions and illustrations from their original publication (table 1). While comparing our fossils, we also revised the type specimen of *Melastomaephyllum danielis* Huert. The age of this fossil was initially interpreted as Eocene (Huertas 1977) and later cited as Oligocene (see Renner

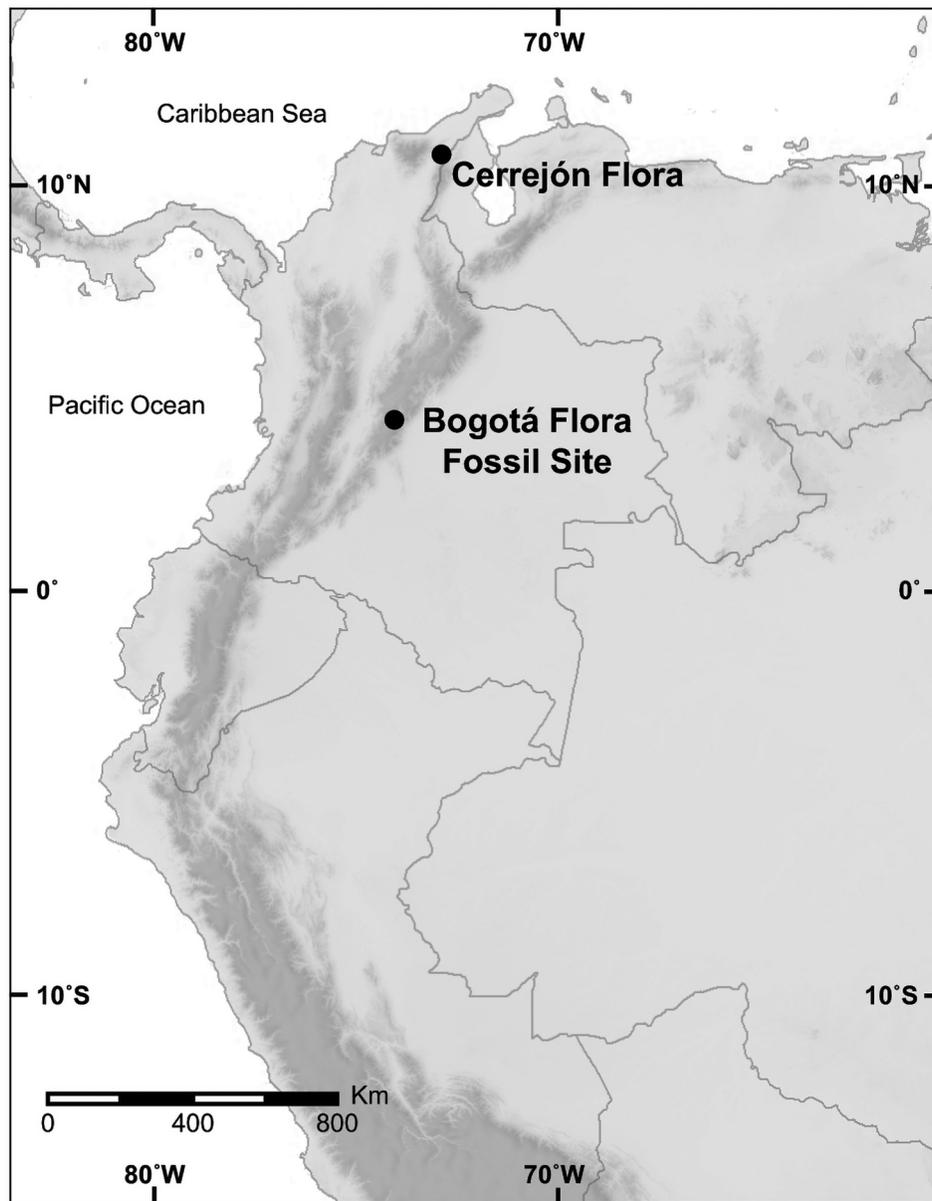


Fig. 1 Collection site for the middle–late Paleocene Bogotá flora at Parque Minero Mochuelo, Cundinamarca, Colombia. Note Cerrejón flora for geographic comparison.

et al. 2001; Fritsch et al. 2004) without much geological detail or reference to a sedimentary unit. We reassessed the age of *M. danielis* using pollen isolated from the rock containing the type specimen. A small fragment of rock was chiseled off without compromising the leaf impression, and it was prepared using a palynological standard method (Traverse 2007) at the Paleoflora laboratory, Bucaramanga, Colombia.

Results

Systematics and Taxonomic Treatment

Order—Myrtales (*sensu* APG VI)

Family—Melastomataceae Juss. (*nom. cons.*)

Subfamily—Melastomatoideae Seringe

Genus—*Xystonia* M. Carvalho *gen. nov.*

Type—*Xystonia simonae* M. Carvalho *sp. nov.*

Generic diagnosis. Leaves petiolate, ovate, untoothed. Apex shape straight, base cuneate. Venation acrodromous with one pair of suprabasal, lateral major veins. Tertiary veins opposite to chevroned percurrent, basally perpendicular to the

midvein. Exterior tertiaries merged forming an intramarginal vein.

Species—*Xystonia simonae* M. Carvalho sp. nov.

Specific diagnosis. Leaves ovate to elliptic, untoothed, coriaceous. Petiole apically furrowed. Lamina with a length-to-width ratio of 3:1, apex shape straight, and base shape cuneate. Venation acrodromous with one pair of suprabasal, well-developed secondaries that are decurrent on the midrib and converge at the apex. Tertiary veins sinuous to chevroned percurrent, basally perpendicular to midrib and becoming acute distally. Exterior tertiaries perpendicular to midrib and forming an intramarginal third-order vein. Fourth-order veins alternate percurrent to ramifying.

Holotype. STRI 45430/MUN P253 (fig. 2A).

Other material. STRI 45369/MUN P81, STRI 45400/MUN P223, STRI 45401/MUN P224, STRI 45404/MUN P227, STRI

45405/MUN P228, STRI 45406/MUN P229, STRI 45407/MUN P230, STRI 45408/MUN P231, STRI 45411/MUN P234, STRI 45413/MUN P236, STRI 45414/MUN P237, STRI 45417/MUN P240, STRI 45420/MUN P243, STRI 45421/MUN P244, STRI 45423/MUN P246, STRI 45424/MUN P247, STRI 45425/MUN P248, STRI 45426/MUN P249, STRI 45429/MUN P252, STRI 45436/MUN P259, STRI 45437/MUN P260, STRI 45466/MUN P284, STRI 45516/MUN P334.

Repository. Museo Mapuka, Universidad del Norte, Barranquilla, Colombia. Museum collection acronym, MUN.

Fossil locality. All leaves come from fossil locality 860015 (lat. 4.5336°N, long. 74.1399°W), situated at Parque Minero Industrial Mochuelo, Bogotá, Colombia (fig. 1).

Stratigraphic position and age. The leaves are middle-late Paleocene in age (58–60 Ma).

Etymology. The name *Xystonia* is derived from “xyston,” a long thrusting spear used in ancient Greece, and makes reference to the distinct spear shape of the leaves. The specific epithet



Fig. 2 Light micrographs of *Xystonia simonae* M. Carvalho gen. et sp. nov. A, Holotype. Elliptical, untoothed leaf with acrodromous venation formed by one suprabasal pair of well-developed secondary veins. STRI 45430/MUN P253. B, Leaf fragment with one pair of suprabasal acrodromous veins. STRI 45407/MUN P230. C, Detail of cuneate, decurrent leaf base. STRI 45400/MUN P223. D, Straight, acute apex. STRI 45466/MUN P284. E, Intramarginal vein formed by tertiary veins. STRI 45369/MUN P81. F, Detail of sinuous tertiary venation and foveate texture. STRI 45425/MUN P248. Scale bars = 1 cm (A–D), 5 mm (E, F).

simonae honors Simona Amaya, a female heroine of the independence of New Granada (nowadays Colombia) from the Spanish crown. Simona, dressing as a man, commanded as sergeant and died in the Vargas Swamp Battle in 1819 (Gómez 2011).

Detailed description. The fossils are notophyllous to mesophyllous leaf impressions (fig. 2A, 2B). The petiole is 0.18–0.28 cm wide and 0.44–0.58 cm long and is adaxially canaliculate (fig. 2C). The leaf lamina is 9.18–13.75 cm long and 3.36–4.45 cm wide and has an ovate to elliptic shape, an acute and straight apex, and a decurrent base (fig. 2C, 2D). The leaf texture is coriaceous and covered by minute foveae that resemble the bases of multicellular hairs, common among Melastomataceae (fig. 2F; Wurdack 1986). The leaf venation is acrodromous, with only one pair of suprabasal secondaries that are decurrent on the primary vein and merge at the leaf apex. The tertiary veins are sinuous to chevroned percurrent and connect the primary with secondary veins (fig. 2F). The angle between the tertiaries and the primary vein is nearly 90° toward the base of the leaf and decreases distally. The exterior tertiaries are consistently perpendicular with respect to the midrib, and they merge to form an intramarginal vein of tertiary gauge (fig. 2E). Fourth-order veins vary between weakly alternate percurrent to ramifying.

Systematic affinity. Perfect acrodromous venation is not common among angiosperms. Only a few lineages aside from Melastomataceae have independently evolved leaves with similar venation patterns, including some species of Lauraceae (i.e., *Cinnamomum* Schaeff.), Smilacaceae, Dioscoreaceae, Piperaceae (*Piper* L., *Manekia* Trel.), Asteraceae (*Mikania* F.W.Schmidt), and Menispermaceae (*Curarea* Barneby & Krukoff). Species of *Cinnamomum* with acrodromous venation differ from *Xystonia* in having looping external tertiary veins (see fig. A1, available online, for morphological comparison). Leaves of *Smilax* L. typically have rounded to cordate bases and more than one pair of lateral major veins, as do species with acrodromous venation of Dioscoreaceae, Piperaceae, and Menispermaceae.

Leaves with perfect acrodromous venation are consistently found among Melastomataceae (Klucking 1989). Within the family, a few species of Olisbeioideae (former Memecylaceae) are occasionally acrodromous (Klucking 1989), whereas acrodromal venation is shared among most Melastomatoideae (Clausing and Renner 2001). The number and position of major veins are variable across the subfamily. Species with acrodromal venation include leaves with one pair of lateral, basal to suprabasal, well-developed secondary or primary veins (fig. 4A, 4B), leaves with multiple pairs of lateral primary veins (fig. 4C), and leaves with various pairs of acrodromal secondary veins that diverge along the primary vein (fig. 4D). Leaves with one pair of well-developed, basal secondary veins are found across various tribes and are therefore likely to have evolved numerous times within Melastomatoideae. This type of leaf typically has an intramarginal vein formed by exterior tertiaries (fig. 4A, 4E–4G) and has a tertiary vein framework that connects the midvein with lateral secondaries and follows one of three distinct patterns: (i) thin, widely spaced, mixed percurrent veins (fig. 4E), frequently seen in leaves of *Pternandra* and members of Astroniae; (ii) well-defined, straight, opposite percurrent veins (fig. 4F, 4G); or (iii) thin, sinuous to chevroned percurrent veins (fig. 4H, 4I), as seen in some species of *Melastoma* L. and *Tibouchina* Aubl.

The leaves of *Xystonia simonae*, characterized by a single pair of basal/suprabasal lateral secondary veins, sinuous percurrent

tertiaries, and an intramarginal vein formed by exterior tertiary veins, are consistent with Melastomatoideae. Because this character combination is not restricted to any particular lineage within the subfamily, we consider *X. simonae* as crown Melastomatoideae. Leaf cuticles were not preserved for *X. simonae*, and therefore epidermal traits are not available for comparison.

Comparison with fossil taxa. Because *X. simonae* differs from all fossil leaves previously attributed to Melastomataceae, we consider that the designation of the new genus is most appropriate for the Bogotá material. Leaves of *Melastomaephyllum* (Geyler) Käusel have notably thick, straight percurrent tertiary veins that contrast with the sinuous tertiary veins of *X. simonae*, and leaves of *Acrovena laevis* differ in having more than one pair of secondary veins that arise along the midvein.

Melastomites Unger is a morphogenus originally described for leaves of Melastomataceae with no clear affinity to a particular genus. Nonetheless, most *Melastomites* either have unconfirmed affinities to Melastomataceae or have affinities to other families (e.g., Renner et al. 2001; Manchester 2014). The traits related to other plants that differ between *X. simonae* and leaves of *Melastomites* are indicated in table 1.

Comments on insect damage preserved on the leaves. *Xystonia simonae* preserves abundant traces of insect-associated leaf damage, including various examples of holes of different sizes (hole feeding DT01, DT03, DT05 of Labandeira et al. 2007), excisions of the lamina along the leaf margin (margin feeding DT12, DT14, DT15), skeletonization (DT17), polylobate patches of leaf surface abrasion (surface feeding DT30), and piercing marks seen as circular punctures on the leaf lamina (piercing and sucking DT46). Three distinct types of leaf galls are also preserved. These are polylobate to elliptical galls, ~1.5 mm wide, with a distinctly striated surface and avoiding major veins (galling DT303; fig. 3A); circular galls, ~2 mm wide, characterized by a thickened core and thickened gall wall that are separated by a featureless area (galling DT49; fig. 3B); and darkened elliptical galls that measure ~1.5 mm long and ~1 mm wide and have multiple central holes 0.2 mm wide (galling DT83; fig. 3C, 3D).

Age and Affinity of *Melastomaephyllum danielis*

The pollen retrieved from the type specimen of *M. danielis* (fig. 5) include *Nijssenosporites fossulatus*, *Laevigatosporites tibuensis*, *Perinomonoletes "reticuloacicularis,"* *Matonisporites* sp., *Psilatriteles* 25–50 μm, *Stephanocolpites* sp., *Clavapollenites* sp., *Retitricolporites* sp. A., *Foveotricolpites* sp., *Clavainaperturites microclavatus*, *Ranunculacidites operculatus*, and *Psilatricolporites garzonii*. These taxa indicate the biozones upper T-12 to lower T-16 of Jaramillo et al. (2011), suggesting an early to middle Miocene age (18.2–11.6 Ma) for this fossil. In his original description, Huertas (1977) indicated that the type specimen was collected in the municipality of Ituango in Antioquia (Colombia), but there was no mention of the sedimentary unit this specimen came from. On the basis of our age estimate and the geology of the area, we interpret that *M. danielis* most likely belongs to the upper segment of the Amagá Formation.

Huertas (1977) described *M. danielis* as resembling various species of *Meriania* Sw., and this taxon has therefore been used to constrain the age of crown Merianiae (Fritsch et al. 2004). Nonetheless, the leaf architecture of the only known specimen of *M. danielis* is also seen in various non-Merianiae taxa of

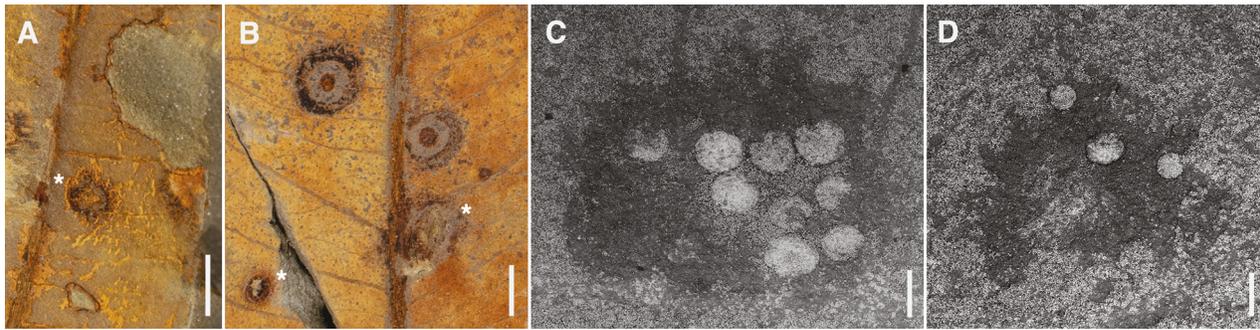


Fig. 3 Light (A, B) and scanning electron (C, D) micrographs showing galling leaf damage in *Xystonia simonae* M. Carvalho gen. et sp. nov. (holotype STRI 45430/MUN P253). A, Polylobate leaf gall with a seemingly woody gall wall and avoiding major veins (galling DT303). B, Two circular galls with a thickened core and thickened gall wall that are separated by a featureless area (galling DT49). C, D, Darkened elliptical galls with multiple central holes (galling DT83). Scale bars = 2 mm (A, B), 200 μ m (C, D).

Melastomataceae, including various species of *Miconia* sensu lato, therefore challenging the natural affinity of this fossil taxon. Given the absence of leaf cuticle and epidermal details that may further support natural affinities, *M. danielis* cannot be unequivocally placed within Merianieae or any other clade of Melastomataceae.

Discussion

Biogeographical Implications

Melastomataceae are mainly pantropical, and their greatest diversity is concentrated in the Neotropics (Stevens 2001–; Veranso-Libalah et al. 2018), yet their early fossil record is centered in North America (Renner et al. 2001). Acrodromously veined leaves, such as *Acrovena laevis*, known from early Eocene deposits of the Golden Valley Formation in North Dakota (Hickey 1977), and undescribed leaves from the Eocene Klondike Mountain Formation in Washington State (currently under study and of uncertain affinity; K. Pigg, personal communication) have been the primary evidence used to support a Laurasian origin for Melastomatoideae (*Pternandra* and all other Melastomaceae s.s. in Renner et al. 2001). The middle–late Paleocene *Xystonia simonae* sp. nov. predates *A. laevis* by 5–7 Ma and indicates a new minimum age of 58–60 Ma for this group. The Paleocene age and Neotropical location of *X. simonae* reject a Laurasian origin (estimated as ~53 Ma) for Melastomatoideae (Renner et al. 2001) and conflict with ages younger than 58 Ma previously obtained from molecular estimates for crown group Melastomataceae (e.g., Wikström et al. 2001; Sytsma et al. 2004). Instead, the South American fossils described here show that Melastomatoideae occurred south of the Tethys Sea by the middle–late Paleocene and better fit with biogeographic interpretations that are based on extant distribution and that consider this lineage as Gondwanan in origin (e.g., Raven and Axelrod 1974; Gentry 1982; Renner 1993; Jacques-Félix 1994; Morley and Dick 2003; Berger et al. 2016).

Berger et al. (2016) reconstructed western Gondwana as the ancestral area for crown Myrtales during the early Cretaceous and proposed a South American origin for the family using a

Bayesian approach (although only a small number of Melastomataceae were included). The only fossil evidence that supported this scenario, instead of an African (Morley and Dick 2003) or eastern Gondwanan (Renner et al. 1993) origin, was the tentative but unconfirmed affinity of *Heterocolpites palaeoceanica* to Melastomataceae, which is often found in Colombian Paleocene deposits (Van der Hammen and García de Mutis 1966; Jaramillo et al. 2011). The occurrence of *X. simonae* in South America confirms the distribution of Melastomataceae (and of Melastomatoideae) in the Neotropics as early as the middle–late Paleocene and indicates a long history for the family in the continent. Younger records of Melastomataceae in South America include *Miconia*- and *Tibouchina*-like leaves from the Eocene–Oligocene Fonseca Formation in Minas Gerais, Brazil (Duarte 1956; Maizatto et al. 2008), leaves from the Miocene Amagá Formation in Colombia (see above; Huertas 1977), and various types of seeds from Pliocene deposits of the Tilatá Formation in Colombia (Wijninga 1996). Ecological shifts allowing the colonization and subsequent radiation in new habitats (i.e., Michelangeli et al. 2013), such as montane cloud forests, paramos, punas, and cerrados, formed by the Andean uplift and cooling global trends throughout the Cenozoic are likely to explain the high diversity of Melastomataceae in tropical South America today (Hoornt et al. 2010).

Although the early occurrence of *X. simonae* coincides with a South American origin for the family, it does not provide definitive evidence for this hypothesis. Testing for ancestral areas using fossils requires an abundant and extensively sampled fossil record. Unfortunately, early records of Melastomataceae are particularly sparse given the difficulty in identifying their pollen (Muller 1981; Patel et al. 1984; Morley and Dick 2003) and the collection bias of macrofloras from Paleogene tropical areas. Despite these limitations, the fossil record of Melastomataceae suggests that this lineage reached North America by the early Eocene, when the warmer worldwide climate (Zachos et al. 2008) and a shallower latitudinal temperature gradient than today (Greenwood and Wing 1995) favored the dispersal of megathermal taxa into higher latitudes. It is possible that the warm climates and dispersal corridors connecting landmasses in the Northern Hemisphere during the Eocene (Tiffney 1985; Tiffney and Manchester 2001) also facilitated the movement

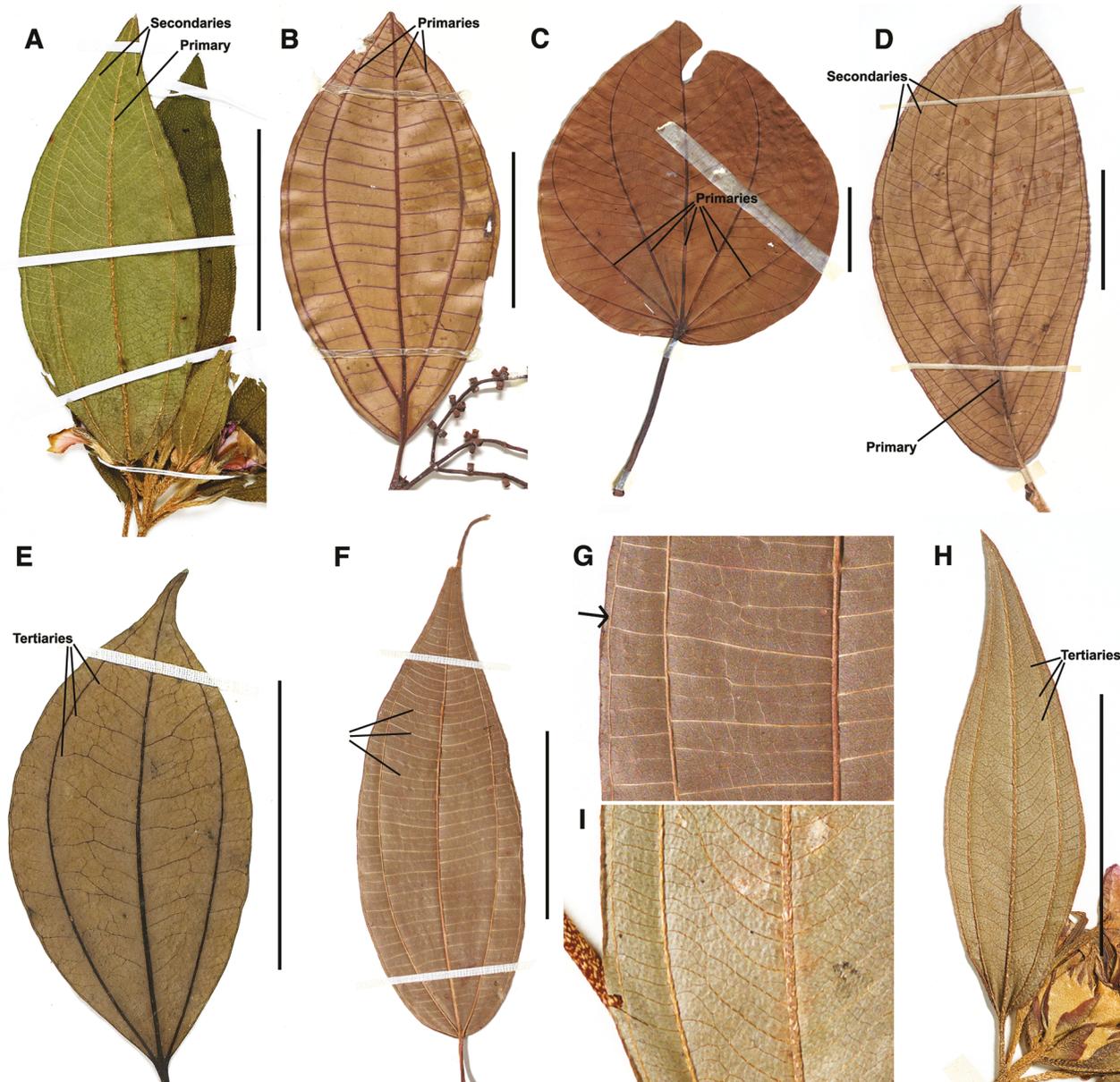


Fig. 4 Photographs showing leaf morphology of acrodromous Melastomataceae. A, Acrodromal venation with one basal pair of lateral, well-developed secondary veins. *Melastoma malabathrichum* L. (US barcode 00965254). B, Leaf with one pair of suprabasal veins that may be considered of primary (width >75% of midrib at divergence point sensu Ellis et al. 2009) or secondary order (diverging from the midrib) following family-specific terminology (Judd and Skeeon 1991). *Miconia fragrans* Cogn. (US barcode 00651465). C, Acrodromal venation with two pairs of basal primary veins. *Graffenrieda latifolia* (Naudin) Triana (US barcode 01013319). D, Acrodromal venation with multiple pairs of secondary veins that diverge along the midvein. *Medinilla disparifolia* C.B. Rob. (US barcode 02928097). E, Thin, widely spaced, mixed percurrent tertiaries in *Pternandra* sp. (US barcode 00940193). F, G, Pronounced, straight percurrent tertiary veins and detail of intramarginal vein (arrow in G) formed by external tertiaries in *Graffenrieda anomala* Tr. (US barcode 02925776). H, I, Sinuous to chevroned percurrent tertiary veins in *Melastoma fuscum* Merr. (US barcode 02921868). Scale bars = 5 cm.

of Melastomataceae into Eurasia during this time. Fossil evidence indicates that by the Miocene, Melastomataceae had a widespread distribution: *Rhexia*-like seeds were abundant in Europe (Collinson and Pinggen 1982), and indeterminate leaves are known from North America (mentioned by Renner et al. 2001), Sumatra (Kräusel 1929), and northern South America (Huertas 1977).

Early Neotropical Rain Forests

Leaf assemblages from the middle–late Paleocene Bogotá and Cerrejón floras are dominated by angiosperms, and their non-monocot leaf physiognomy resembles that of warm tropical rain forests in having numerous large, untoothed leaves and abundant leaves with drip tips (Wing et al. 2009). These Paleocene

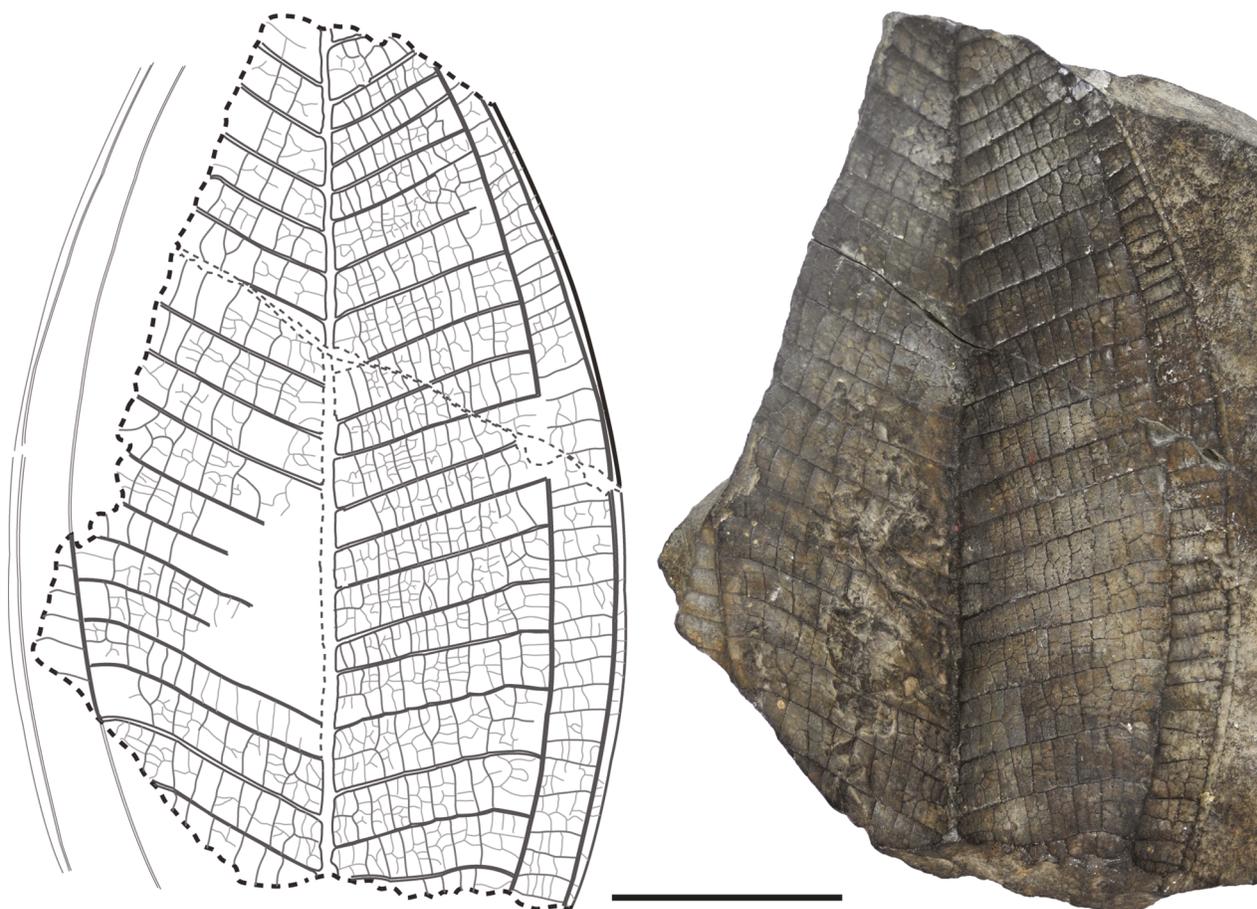


Fig. 5 Line drawing and light micrograph of *Melastomaephyllum danielis* Huert. Holotype. Scale bar = 5 cm.

forests also indicate having a multistratal canopy structure (Crifo et al. 2014; Graham et al. 2019) and abundant plant-insect interactions, and most significantly, these are the earliest forests to have the same plant family composition shared by modern Neotropical rain forests (Burnham and Johnson 2004; Wing et al. 2009). Melastomataceae is the fourth-most diverse family of vascular plants in the Amazon today (Cardoso et al. 2017), yet the family had not been previously confirmed within Paleocene deposits (although it had been suggested on the basis of tentative affinities of pollen; Van der Hammen and García de Mutis 1966). The occurrence of Melastomataceae in the Bogotá Formation conforms to the general pattern in which dominant and diverse plant lineages in the Neotropics today were also abundant or have their earliest occurrences in the Paleocene tropics (Doria et al. 2008; Herrera et al. 2008; Gomez-Navarro et al. 2009; Carvalho et al. 2011; Herrera et al. 2011, 2019; Stull et al. 2012). This new familial record indicates the role of Melastomataceae in the early assembly of Neotropical rain forests during the Paleocene and highlights a potential bias in the fossil record of tropical taxa.

Paleoecological Remarks

The middle-late Paleocene (58–60 Ma) rain forests of Bogotá are roughly coetaneous and share a similar paleoclimate, phys-

iognomy of nonmonocot leaves, and plant family composition as the Cerrejón flora (58–60 Ma; Wing et al. 2009), where families and lineages such as Fabaceae, Areaceae, Araceae, Lauraceae, Malvaceae, Euphorbiaceae, and Zingiberales dominate the leaf biomass. The Bogotá flora also contains abundant legume pods (Herrera et al. 2019) and fruits and seeds of Annonaceae, Passifloraceae, Menispermaceae (Herrera et al. 2011), and Icacinaeae (Stull et al. 2012). Of leaf taxa in the Bogotá flora, 54% have untoothed margins, 62% are mesophylls or larger, and 6 of 20 leaf types with preserved apices have drip tips, whereas in the Cerrejón flora, 76% of leaf morphotypes have untoothed margins, 68% are mesophylls or larger, and 12 of 34 leaf types have drip tips. Estimates of mean annual rainfall based on leaf area analysis indicate annual precipitation (Wilf et al. 1998; Peppe et al. 2011) of 182–184 cm yr⁻¹ for the Bogotá flora and 324 cm yr⁻¹ for the Cerrejón flora (Wing et al. 2009), indicating comparable precipitation regimes between the two sites.

Although the family-level dominance is similar in Bogotá and Cerrejón, Melastomataceae has not been found in the thoroughly studied Cerrejón flora. Only 23% of leaf taxa at Bogotá are also present in Cerrejón, potentially reflecting ecological distinctions between both sites. Well-developed paleosols and carbonate nodules in the Bogotá Formation (Morón et al. 2013) are indicative of better-drained soils than in the coastal, waterlogged environments

of the Cerrejón Formation. In modern rain forests, soil-related properties, such nutrient content and water availability, have a profound effect on the floristic and functional composition of plant communities (Engelbrecht et al. 2007; Jirka et al. 2007; John et al. 2007; Condit et al. 2013; Schiatti et al. 2014). Edaphic differences and susceptibility to waterlogging could potentially explain the restricted occurrence of *X. simonae* in the well-drained, inland environments of Bogotá.

Three distinct gall types were observed on a single specimen of *X. simonae* (fig. 3), and abundant leaf chewing damage types are preserved in the leaves. This observation matches the high abundance and diversity of leaf damage found in the Bogotá flora, which contrasts with the abundant but depauperate leaf damage diversity in the rain forests of Cerrejón (Giraldo et al. 2021). Leaf galling is a highly specialized, host-specific interaction mostly induced by insects but also related to viruses, bacteria, nematodes, and mites. Living Melastomataceae have a high diversity of galling interactions in tropical rain forests, the Atlantic Forest, and Brazilian coastal and cerrado ecosystems, where species of the family are hosts to midges (Diptera: Cecidomyiidae), psyllids (Hemiptera: Psyllidae), lepidopterans, coleopterans, mites (Acariformes: Eriophyidae), and nematodes (Tavares 1917; Burckhardt and De Queiroz 2012; Santos et al. 2012, 2014; de Araújo et al. 2014; Julião et al. 2014; Maia et al. 2014). In fact, most lepidopteran galls described from South America are found in species of Melastomataceae (Maia et al. 2014). The gall morphol-

ogies preserved on *X. simonae* match with galls induced by mites (DT303; fig. 3A), psyllids (DT49; fig. 3B), and midges (Cecidomyiidae; DT83; fig. 3C, 3D; Labandeira et al. 2007 and subsequent updates). These fossilized galling records reveal that the highly specific interactions seen between gall-forming organisms, which can have negative feedback on Melastomataceae leaves, evolved at least since the middle-late Paleocene. Whether *X. simonae* evolved any chemical and or physical defenses against those gall-forming organisms remains unknown.

Acknowledgments

We thank Ladrillera San Marcos for allowing access to the fossil site, A. Idárraga for granting access to the collections of JAUM, Hno J. Espitia Barrera and the Museo de La Salle in Bogotá for allowing sampling of the holotype of *Melastomaephyllum danielis*, F. Michelangeli for discussions on fossil affinities, J. Ceballos at STRI for SEM support, A. Rincón and A. Reyes-Céspedes for their help with fossil collections, Museo Mapuka for facilitating access to fossil collections, Universidad del Norte for facilitating access to research facilities, and K. Pigg and two anonymous reviewers for their helpful comments. This research was funded by NSF grant EAR-1829299 to M. R. Carvalho, F. Herrera, and C. Jaramillo; an Earl S. Tupper postdoctoral fellowship to M. R. Carvalho; and the Oak Spring Garden Foundation to F. Herrera.

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