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Synonymized classification of leaf domatia: a comprehensive survey of Neotropical Melastomataceae

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Table 1 is available in the Supplementary Files section.

Synonymized classification of leaf domatia: a comprehensive survey of Neotropical Melastomataceae

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Abstract: Domatia are structures on plants that facilitate a mutualistic symbiosis; domatia provide a sheltered habitat for other organisms, and plants with domatia receive some benefit from the presence of the organisms. Large, ant-inhabited domatia have been the focus of the majority of domatium studies thus far, while smaller leaf domatia not inhabited by ants have historically been overlooked. Inhibiting their study is the fact that no comprehensive species-level survey has been completed, and a functional morphological classification is lacking. The plant family Melastomataceae includes hundreds of species with these leaf domatia which represent a unique level of morphological diversity, particularly in the Neotropics. Here, we

utilize herbarium specimens and literature to conduct a thorough survey of leaf domatia across Neotropical Melastomataceae. In doing so, we investigate the boundaries of what should be considered a domatium. We identify small leaf domatia in 568 species, 331 more than previously reported in the literature reviewed here. We also record the absence of domatia in 2536 species and summarize domatium diversity across Neotropical tribes of Melastomataceae. Ultimately, we present a comprehensive photo glossary and illustrated key of putative domatia. This classification, which synonymizes 50 existing terms, can be utilized not only in Melastomataceae, but across vascular plants. Finally, we provide preliminary evidence for the use of these structures by mites and other invertebrates.

Keywords: Herbarium collections; invertebrates; leaf domatia; mites; mutualism; symbiosis.

Introduction

Background

Interactions between plants and animals are significant drivers and maintainers of global biodiversity: Pollination is responsible for rapid radiations in insect and plant diversity (Stebbins, 1970; Peris & Condamine, 2024), seed dispersal is a major enhancer of community diversity (Cadotte, 2006), and herbivory has driven the evolution of thousands of novel chemical defenses in plants (Futuyma & Agrawal, 2009). A lesser-understood interaction occurs in leaf domatia, small structures on plants that house invertebrates and other organisms. Leaf domatia have evolved hundreds of times across at least 105 plant families and are estimated to occur in ca. 10% of all woody angiosperms (Myers et al., 2024). Because of their prevalence across the plant kingdom, leaf domatia have likely played, and continue to play, a significant role in the ecology and evolution of plants and invertebrates.

The plant family Melastomataceae harbors an impressive number of species with domatia, particularly in the Neotropics. Domatia that house ants, often referred to as "myrmecodomatia," have been described from the leaves, stems, and pseudostipules of ca. 75 species of Neotropical Melastomataceae (Michelangeli, 2005, 2010). Myrmecodomatia are typically ≥1 cm in length (Michelangeli, 2010) and thus discernible without magnification, resulting in their relatively thorough study. In several species, domatia have been shown to facilitate a mutualism in which ant inhabitants protect the plant from herbivory by other invertebrates (Morawetz et al., 1992; Alvarez et al., 2001; Bizerril & Vieira, 2002; Michelangeli, 2003), and even provide nutrients for the plants (Cabrera & Jaffe, 1994; Solano & Dejean, 2004).

Smaller leaf domatia, typically <1 cm and not possessing ants, are known to occur in at least 88 species of Melastomataceae, making them the fourth-ranked plant family in number of

domatia-bearing species, following Rubiaceae, Sapindaceae, and Combretaceae (Myers et al., 2024). Small leaf domatia in Melastomataceae are also particularly morphologically diverse compared to these other families (Fig. 1). In the tribe Pyxidantheae alone (204 species), at least nine unique morphologies have been observed (Penneys & Judd, 2011; Wieser, 2025).

Current state of knowledge

Non-ant leaf domatia are often referred to as "acarodomatia" (Lundström, 1887), mites being the presumed inhabitants. However, while mites have been observed in some small leaf domatia in Melastomataceae (Almeda, 1989; Pemberton & Turner, 1989; Skean, 1993; Wieser, 2025) and other plant families (O'Dowd & Willson, 1989; Pemberton & Turner, 1989; Romero & Benson, 2004), many non-mite arthropods have been observed too (O'Dowd & Willson, 1989; Gutiérrez-Duque & Posada-Herrera, 2025; Wieser, 2025). In *Pavetta* L. (Rubiaceae), leaf domatia apparently even house beneficial bacteria (Bremekamp, 1937). Thus, Schnell et al., (1968) justly highlighted the bias of the term "acarodomatia" in reference to all small leaf domatia. Accordingly, we avoid the term here, and suggest it be used only in reference to domatia in which mites are the confirmed symbiotic partners.

In the few Melastomataceae taxa where mites have been observed in small leaf domatia, species-level identification and ecological observations of mites have been severely limited due to their microscopic size and tendency for cryptic speciation (Walter & Proctor, 2013; Skoracka et al., 2015). Further, mite diversity is significantly underdescribed; with an estimated 1,000,000 species on Earth, only 6.3% of these have been described (Sullivan & Ozman-Sullivan, 2021). In light of these challenges, domatia-dwelling mites have historically been identified to family or genus, then based on taxonomy, grouped by diet, i.e., predaceous or fungivorous.

Predaceous mites have been observed in the domatia of several Melastomataceae taxa (Almeda, 1989; Pemberton & Turner, 1989; Skean, 1993). It is assumed that predaceous mites are protecting plants by feeding on herbivorous invertebrates and their eggs. These observations, consistent with the symbioses of ant domatia in the family, have been referred to as the "bodyguard" (Lubbock, 1877) or "standing army" (Belt, 1874) hypotheses. However, scavenger mites, which feed on fungi and bacteria, have been observed in the domatia of *Miconia birimosa* (Naudin) Skean, Judd & Majure (Skean, 1993). These findings may represent another type of symbiosis in which mites serve as "housekeepers," cleaning leaves of fungi and other pathogens.

Not only have mites been observed in small leaf domatia of Melastomaceae, but mite eggs have been found in some species, suggesting that domatia may serve as nurseries for mites (Pemberton & Turner, 1989). In other plant families, molting mites and empty mite exoskeletons have been observed in domatia, indicating that mites may complete all or particular parts of their life cycles there (Walter & O'Dowd, 1992; Grostal & O'Dowd, 1994). Consideration of the functional purpose of a domatium brings us to a critical examination of their definition, for which a consensus is currently lacking.

Outstanding questions

Domatium, from the Greek δομάτιον, meaning "little house" or "bedroom" was first defined by Lundström (1887) as "all special structures on a plant part, or modifications of such, that are intended for other organisms which, as mutualistic symbionts—that is, organisms that "stand in a relationship of mutual benefit to the hosts they inhabit"—undergo a significant part of their development there" (translated from the original German). A more comprehensive review of domatia was not published until nearly a century later, when Stace (1965) highlighted domatia

as an underutilized taxonomic character, and identified a significant gap in knowledge on the subject. Stace's definition, "a small cavity of varying form, found on almost any part of the plant, which is inhabited, or thought to be inhabited, by some type of animal," largely agrees with Lundström's. Notably, however, Stace's definition is morphologically restricted (*cavities*), and functionally broader (*potentially inhabited)*. Further, mutualism is not explicit in Stace's description, as it is in Lundström's.

Although a functional definition of domatia, that is, one defining any "space," "special structure" or "modification of such" is useful in some contexts, defining what constitutes each of these presents an additional challenge. For example, in a broad sense, any space that a mite may opportunistically utilize on a plant would then be considered a domatium. Jacobs (1966), discussing mites crawling into crevices in bark, argues that these spaces "have nothing further in common, except that a mite may enter them by chance." Thus, Jacobs advocated for a definition of domatia that would restrict them to structures present only between the axils of the veins. However, Jacobs himself lists several exceptions to this spatial circumscription, and one of the most commonly cited examples of domatia today, ant-inhabited spines of many *Acacia* Mill. species (Belt, 1874), would violate these boundaries as well.

Clearly, attempts to define the boundaries of domatia have proven difficult. However, the necessity of an explicit boundary is questionable, as restricting our definition could hinder our understanding of plant-invertebrate relationships. Specifically, while "special structures" which have been historically identified as domatia may represent conspicuous symbioses between invertebrates and plants, several other leaf traits provide habitats conducive to the same, or similar protection as domatia: indumentum, raised veins, scales, pouchy leaf tissue, etc. As Walter (1996) explains, these morphologies also serve as equally as good "hiding places" for a

mite. Interestingly, domatia are apparently less common in species that have consistent indumentum, presumably because the hairs may serve the same function of protection as domatia (Walter, 1996; Judd et al., 2022). Even when a seemingly "special structure" has been identified, it is not always clear if it indeed houses symbiotic invertebrates. In such cases, the term "pseudodomatia" has been employed (Skean, 1993). However, the original use of the term "pseudodomatia" was in reference to a plant part that did not represent a specialized structure (i.e., an enlarged bulb), but which was being opportunistically utilized by invertebrates (Bailey, 1922).

While it has been disputed what exactly should be considered a domatium, efforts have been made to classify types of putative domatia. Stace (1965) recognized four main types of domatia: *marsupiform, lebetiform, hair tuft,* and *revolute*. Jacobs (1966) recognized the first three of these four, albeit some under different terms (*pocket, pit, and tuft*, respectively), as well as a fourth type, *dome*. As illustrated through this example, there have been notable inconsistencies in terminology used to describe putative domatia, both within Melastomataceae and across plants. One common type of leaf domatium characterized by thin tissue stretched between veins, and here referred to as *marsupiform* (Figs. 1A, 1I), has been referenced under at least twelve varying terms *(marsupiform, marsupiform pocket, membrane, membrane pocule, pocket, pocket-like, poculate, pocule, laminar, small cavity, webbed, pouch*). Further complicating the matter, some of these same terms have also been used to refer to different domatium morphologies in Melastomataceae, e.g., *cavity* (Bécquer et al., 2022; Wieser, 2025) and in other families, e.g., *pocket* (Kim & Ngondya, 2010). Inconsistent terminology presents issues not only for taxonomy and identification within Melastomataceae, but it also prevents meaningful comparative study of domatia across other plant groups too.

The domatium types described by Stace and Jacobs all occur in Melastomataceae, as do at least six other types. Judd & Skean (1991) later described *conical* domatia, Judd et al. (2008) coined the term *apical* domatia, and Penneys and Judd (2011) illustrated *lateral laminae*, *pinwheel*, *petiolar flap*, and *coalesced vein* domatia. The unique diversity of domatium morphology in Melastomataceae, much of which is not captured in existing classifications, presents an even more compelling reason to categorize domatia across the family. Further, Penneys and Judd (2011) identify "hybrid" or "multiple" forms occurring in a single species, which Jacobs (1966) also alluded to: “frequently domatia are nothing but a pit, a pocket, a tuft, or a dome, but not seldom a combination is involved.” Current classifications fail to accurately account for these combinations of morphologies. In addition to discrepancies in terminology, presence and absence data for domatia in Melastomataceae is far from complete. Only 7% of all Neotropical species have officially been categorized as possessing or lacking small leaf domatia (Myers et al., 2024), resulting in a fragmentary picture of domatium diversity across the family.

Given their overall lack of study, poorly defined circumscription, and unclear morphological classification, it follows that the literature surrounding small leaf domatia is fraught with ambiguities. Until small leaf domatia are patiently and thoroughly investigated, question marks will remain.

Objectives

Without a thorough understanding of domatium diversity in Melastomataceae, process-level ecological and evolutionary investigations of these unique structures are seriously limited. In turn, the interconnected conservation of species with domatia, and the invertebrates that may rely on them, is ill-informed. In this study, we a) provide a vouchered species-level dataset of

leaf domatia in Melastomataceae, b) introduce a synonymized morphological classification of domatium morphology, and c) present preliminary evidence for invertebrate use of domatia.

Materials & Methods

Literature review

A list of all accepted species of Melastomataceae in North and South America was downloaded from Plants of the World Online (POWO, 2024). This dataset was cross-referenced with a expert-validated list of accepted species to account for new species and synonyms not captured in POWO (Michelangeli et al., 2020). A literature search for domatia in Melastomataceae was conducted in Google Scholar using the key words: Melastomataceae AND acarodomacios OR acarodomatia OR domacios OR domatia OR mites. Using the available literature, domatium presence or absence was recorded in the species list. If specific terminology or descriptive language was used to refer to domatium morphology, this information was recorded as well. Foreign language terms were synonymized when they had a direct, unambiguous equivalent in English (e.g., *laminar* vs. *laminares*). Original foreign language terms were retained when interpretation could collapse meaningfully different terminology (e.g., *pelos setosos*).

Survey

A survey of leaf domatia was conducted of all Neotropical Melastomataceae species in the William and Linda Steere Herbarium (NY) at the New York Botanical Garden. Any species with a leaf structure similar to those described in the literature, or other obvious leaf structure which could serve as a shelter for an invertebrate, was targeted for further study. If there were

multiple specimens of a single species available, several specimens were examined across a geographic range to confirm domatia presence or absence. Each species examined (both domatia present and absent) is represented by at least one voucher under its barcode number, or collector and collector number if a barcode was not available. Specimens with multiple intact and visible leaves, as well as a recent determination, were prioritized as vouchers. Species not represented in the collection, or species only represented by specimens which did not have an intact or accessible leaf surface, were excluded from the survey and are indicated as such in Appendix 1.

If there were presence/absence incongruencies between the physical specimens and the literature, the vouchered specimens were prioritized unless the literature was a protologue or taxonomic revision. In these cases, images of type specimens from JSTOR Global Plants were examined to resolve inconsistencies between the literature and NY herbarium specimens. Type specimens at NY were also always prioritized in the validation of domatia presence and morphology. Any inconsistencies between non-type specimens and the literature, as well as any inconsistencies between type specimens and the literature, are noted in Appendix 1.

If domatia were present in one reliably identified specimen, but absent in another, or if domatia were developed on some leaves of a specimen but absent on others, domatia were considered variable, and indicated by an asterisk next to the domatia type in Appendix 1.

In addition to documenting domatia presence or absence for every available species, several other leaf traits that could serve as suitable invertebrate habitat on the abaxial leaf surface were recorded: presence of indumentum, raised midvein and secondary veins, depressed laminar tissue between veins, rolled leaf margins, large scales over the vein axils, webbed hairs in the vein axils, and a leaf base that extends over or overlaps the petiole. Because many species of

Melastomataceae are known to possess ant domatia, the presence of ant domatia, verified by ants or ant nests, was also recorded.

Morphological classification

All specimens which were targeted for further study were then grouped into morphological categories based on their domatia or domatia-like structures. If a species exhibited more than one type of structure (e.g., webbed tissue between veins *and* a concentration of hairs between veins), then both morphologies were recorded. Terms and descriptive words from the literature search were reviewed to account for prior names for domatia, given that an image or illustration was provided that could confirm the shared morphology. If a term from the literature was morphologically representative, and also had not been used to describe other types of domatia, then it was retained as the accepted term. Descriptive definitions of each domatia type were developed, and other terms used in the literature were synonymized under each definition.

Imaging

Vouchers of all species bearing domatia, and many vouchers of species not bearing domatia, were imaged on Nikon SMZ1500 stereoscope with a DXM1200F camera attachment. Several vouchers were also coated in gold-palladium with a Denton DSK00V-0016 sputter coater at 15 kv for six minutes, then imaged on a Hitachi SU3500-VP scanning electron microscope (SEM) using accelerating voltages from 5–10 kV. Type specimens were mostly imaged with a Canon EOS R7 with a 67 mm macro lens, and in a few cases when higher quality imaging was not available, an iPhone 11 through a Bausch & Lomb 10× stereo dissecting microscope. All live field photos were taken by F.A. Michelangeli with Nikon cameras (D800,

D810 or Z7ii) using either an AF Micro-NIKKOR 60 mm f/2.8D lens or a NIKKOR Z MC 105 mm f/2.8 VR S lens. All other photos are labeled according to the author's first and last initials.

Results

The downloaded list of Melastomataceae in North and South America from POWO amounted to 3,814 accepted species. Upon cross-referencing the POWO list with the expert-validated list, 24 names from the POWO list were excluded or synonymized, and 60 names were reinstated or added. The final list used for the survey amounted to 3,850 species. The literature search yielded 83 publications with domatium presence/absence data spanning the years 1903–2025. From the literature, domatium presence/absence, and if possible, type of domatium, was recorded for 734 species. After translating direct linguistic equivalents into English, we identified 50 distinct terms referring to domatium morphology.

The survey of NY herbarium specimens resulted in 3,125 species with vouchered presence/absence data. There were 54 species for which no NY specimens were available, but for which literature, loaned specimens, and/or type images confirmed domatium presence/absence. Information and/or specimens were not available for 663 species, and findings were unclear for eight species. In total, domatium presence/absence was recorded for 3,179 species, representing 83% coverage of the 3,850 accepted Neotropical species.

Imaging resulted in 1,402 photos and 121 SEM images of 660 species. Images are available at https://sweetgum.nybg.org/science/projects/melastomataceae/, where they are linked to their accessioned NY herbarium records. Images can be queried by a keyword search for "domatia", or by searching the specimen barcode number listed in Appendix 1.

We found 643 species of Neotropical Melastomataceae with specialized leaf structures that, according to existing literature and our own observations, should be considered domatia, or

at least, potential domatia. Of these, 75 species possess ant domatia according to the literature, their larger size, and/or the presence of ants or ant nests on specimens. Within the 568 remaining species with smaller, non-ant leaf domatia (from here on referred to as leaf domatia), we identified ten distinct morphologies: *apical, marsupiform, petiolar, pinwheel, pit, recessed, revolute, tuft, venous,* and *volcano* (see Glossary (Figs. 2–13); Fig. 14; Fig. 15). Two of these terms, *recessed* and *venous,* are newly proposed here. Additionally, three new subtypes are presented: *marsupiform ciliate, marsupiform inflated,* and *marsupiform fissured.* Under this new classification, 50 terms from the literature are synonymized. Additionally, we include information regarding if mites or other invertebrates have been observed utilizing these structures, either from the literature or our own observations.

Glossary

***Apical*:** rolling of the apex of the leaf margin towards the leaf adaxial surface to form a hollowed, conical structure (Fig. 2). Rare; only recorded in two species of *Henriettea* DC. No invertebrates have been observed.

= *apical* (Judd et al., 2008; Carmenate-Reyes et al., 2017)

***Marsupiform*:** membranaceous tissue between veins that forms a sheltered space between the tissue and the leaf surface (Fig. 3). Sometimes well-developed and consistent, other times inconspicuous and inconsistent within a species and/or individual. Can occur only between primary and secondary veins, or across several veins in many-plinerved species. Often occurs with *recessed* or *tuft* morphology, and can be variable in its own morphology: *ciliate marsupiform*, or *fissured marsupiform*, or *inflated marsupiform* (Fig. 3). Mites and other

invertebrates have been observed in *marsupiform, marsupiform ciliate,* and *marsupiform inflated* domatia.

= *marsupiform* (Skean, 1993; Baumgratz, 1997; Liogier, 2000; Judd, 2007; Silva & Baumgratz, 2008; Kriebel et al., 2015; Justino et al., 2016; Santos et al., 2022); = *pocket* (Penzig & Chiabrera, 1903; Almeda, 1989, 2009; Brouwer & Clifford, 1990; Kriebel, 2016; Myers et al., 2024); = *marsupiform pocket* (Penneys & Judd, 2011; Wieser, 2025); = *membrane* (Martins, 2009; Caddah & Goldenberg, 2013); = *membrane pocule* (Gamba & Almeda, 2014); = *pocket-like* (Almeda, 2009); = *poculate* (Almeda, 2001, 2009); = *pocule* (Alvear & Almeda, 2019)*;* = *laminar* (Baumgratz, 2004; Paredes Burneo, 2019); = *small cavity* (Bécquer et al., 2022); = *webbed* (Howard, 1989)*;* = *pouch* (Judd & Penneys, 2004)

Marsupiform ciliate: marsupiform with hairs along the margin of the webbed tissue (Fig. 4A).

Marsupiform inflated: marsupiform that forms a well-developed dome or pouch (Fig. 4B). Often variable in development (i.e., some leaves are regular marsupiform, others appear inflated).

= *vesicular pocket* (Kriebel, 2016); = *open pocket* (Penneys & Judd, 2011); = *domed pocket* (Brouwer & Clifford, 1990); = *thickened poculate* (Almeda, 2009); = *gall-like* (Skean et al., 2018); = *pouch* (Larcher de Carvalho et al., 2012); = *well-developed pocket* (Almeda, 2009); *small hole* (Bécquer et al., 2022)

Marsupiform fissured: marsupiform with an irregular margin (Fig. 4C). Unclear if this fissuring occurs early on, or as the leaf grows and develops.

***Petiolar*:** tissue that overlaps with the petiole adaxially to form a flap-like sheltered area (Fig. 5). Rare; only observed in four species. Invertebrates have not been observed.

= *petiolar* (Baumgratz, 1997, 2004); = *petiolar flap* (Penneys & Judd, 2011; Wieser, 2025)

***Pinwheel*:** flaps of tissue protruding on both sides of the primary and secondary veins (Fig. 6). Differentiated from marsupiform in the presence of tissue on the distal edges of the secondaries, as well as the absence of connected tissue in the very base of the vein axil. In younger leaves, the flaps may only be present between the primaries and secondaries (Fig. 1L photo). Only found in *Chalybea* Naudin. Invertebrates have not been observed.

= *pinwheel* (Penneys & Judd, 2011; Wieser, 2025); = *tissue flaps* (Morales-Puentes & Penneys, 2010); = *lateral laminae* (Penneys & Judd, 2011; Wieser, 2025).

***Pit*:** tissue, often differentiated in color from the rest of the leaf surface (see Fig. 7A) that forms a canopy in the axils of the primary and secondary veins, with a hole of varying sizes, nested within this tissue. Can be quite cryptic, especially on younger leaves, where the hole has not yet fully developed. In one species (see Fig. 7C) the pit appears to develop on the margin of the leaves. Mites and other invertebrates have been observed.

= *pit* (Myers et al., 2024); = *recessed pit* (Penneys & Judd, 2011; Almeda, 2013; Wieser, 2025); *ruptured* (Almeda, 2009); = *slitlike pit* (Almeda, 2009); = *perforated pit* (Almeda, 2009); = *lebetiform* (Stace, 1965); = *bowl-shaped* (Stace, 1965)

***Recessed*:** leaf tissue that is adaxially depressed to create a hollow in the vein axil (Fig. 8). Few species exhibit solely *recessed* morphology; it is often coupled with *marsupiform*, *tuft*, or *venous*

morphology (Fig. 9). Best visualized by viewing the adaxial surface of the leaf, which shows protruding laminar tissue, sometimes of slightly differing colors from the rest of the leaf surface. Invertebrates have been observed in *recessed marsupiform* domatia.

= *vesicular* (Michelangeli et al., 2015); = *depression* (Goldenberg & Chagas, 2014); = *cavity* (Paredes Burneo, 2019; Wieser, 2025)

***Revolute*:** a rolling or folding of the basal leaf margin resulting in a sheltered area below a flap of tissue (Fig. 10). Invertebrates have not been observed.

= *revolute (rolled margin)* (Stace, 1965); = *revolute pseudodomatia* (Skean, 1993; Liogier, 2000; Skean et al., 2018) = *revolute margin* (Michelangeli & Ulloa Ulloa, 2013).

***Tuft*:** a concentrated, often dense, area of hairs in the vein axil (Fig. 11). Most often occurs in the axil of the primary and secondary veins, but can also be found at the junction of primary and tertiary veins too. Often, the rest of the abaxial leaf surface lacks pubescence (Figs. 11A & 11B). If the surface does have pubescence, the hairs of the tuft domatia can then be differentiated by size, color, and/or density (Fig. 11C). Mites have been observed.

= *tuft* (Stace, 1965; Judd & Skean, 1991; Penneys & Judd, 2005; Almeda, 2009; Martins, 2009; De Santiago Gómez, 2010; Judd et al., 2014, 2015; Majure et al., 2014, 2016; Michelangeli & Goldenberg, 2014; Kriebel et al., 2015; Michelangeli et al., 2015; De Santiago Gómez & Michelangeli, 2016; Kriebel, 2016; Mendoza-Cifuentes & Posada-Herrera, 2018; Myers et al., 2024; Gutiérrez-Duque & Posada-Herrera, 2025); = *hair tuft* (Judd, 2007; Penneys & Judd, 2011; Wieser, 2025); = *comose* (Goldenberg & Reginato, 2009); = *concentration of trichomes* (Goldenberg et al., 2021) = *groups of hairs* (Liogier, 2000); = *hairs* (De Santiago Gómez, 2010); = *pelos setosos* (Paredes Burneo, 2019); = *pilose* (De Santiago Gómez, 2000)

***Venous*:** where the meeting of the primary and secondary veins form a cavernous space (Fig. 12). Differs from normal raised veins by the fact that there is a hollow space underneath the meeting of the veins, not just between them. Common in species where the veins are very thick and/or ridged. *Venous* domatia most often co-occur with *recessed* morphology (i.e., *recessed venous*), which deepens the cavernous space. Invertebrates have not been observed.

= *coalesced veins* (Penneys & Judd, 2011; Wieser, 2025)

***Volcano*:** fused tufts of hairs that form a conical structure with an opening at the top (Fig. 13). In some species, *volcano* domatia often occur at multiple vein junctions on a single leaf (Fig. 13C), which is rarely seen in other types of domatia. Invertebrates have not been observed.

= *volcano-like* (Judd et al., 2022); = *groups of hairs* (Liogier, 2000); = *connate hairs* (Judd & Skean, 1991); = *conical* (Judd & Skean, 1991).

Of the two subfamilies of Melastomataceae that occur in the Neotropics, Olisbeoideae and Melastomatoideae, leaf domatia are only found in Melastomatoideae. Of the 19 tribes of Melastomatoideae occurring in the Neotropics, leaf domatia are found in twelve of them (Table 1). Domatia were not found in the tribes: Astronieae, Dissochaeteae, Lithobieae, Rhexieae, Rupestreeae, Sonerileae, and Trioleneae. Marsupiform morphology is the most common type across the subfamily (335 species), and the only type that is shared across the twelve tribes with domatia.

Of all Neotropical Melastomataceae, 2,866 species possess at least one leaf character we consider conducive to suitable mite or other invertebrate habitat. Raised veins on the abaxial leaf surface create sheltered areas where invertebrates were often observed nestled against or underneath (Fig. 16A). When secondary veins are present and also raised, recorded in 2,706 species, the space between primaries and secondaries creates an even more sheltered microhabitat, where invertebrates, fungi, nests, and even cocoons (Fig. 16B) were observed on specimens.

The presence of indumentum on the abaxial leaf surface also appears connected to invertebrate utilization. Mites were spotted on several specimens lacking obvious domatia but with some sheltered areas created by dense hairs (Fig. 16C and Fig. 16F). In several species, a distinct type of webbed indumentum between veins was noted that can sometimes resemble marsupiform or tuft domatia (Fig. 16D). However, this indumentum is inconsistent and seemingly caducous, and as such only included with the other potential invertebrate habitat categories.

Another leaf character where invertebrates were observed taking shelter is under an overlapping or peltate leaf base (Fig. 16E). The presence of wide scales, consistently paired and

spreading over the vein axils (Fig. 16F) is common in several genera within the Melastomateae: *Tibouchina* Aubl.*, Pleroma* D.Don.*, Andesanthus* P.J.F.Guim. & Michelang., and *Pterolepis* (DC.) Miq. We see very little functional difference between this morphology and some marsupiform domatia. Similarly, some species possess particularly small, cupped-shaped leaves, often with indumentum (Fig. 16G). Each leaf offers a sheltered hiding place perhaps functionally indistinguishable to a *recessed tuft,* for example.

Other characters observed closely resemble the domatia types described above, but do not quite fit in these categories. For example, nearly every species of *Axinaea* Ruiz & Pav. exhibits some degree of rolling in the leaf margin (Fig. 16H). In general, we considered this a revolute domatium if the tissue rolled or folded so much that it was at certain points, parallel to the leaf surface. Otherwise, we place it in the non-domatium revolute margin category. While many species across the family appear to have rolled margins in herbarium specimens, we recognize that some species naturally dry this way, and may not exhibit this same degree of rolling while fresh. Similarly, many species were found to have slightly pouched tissue between the veins representing a gradient between flat tissue and recessed domatia (Fig. 16G). Together, these characters blur the lines of domatia, and underpin the need for further investigation.

Several other structures were targeted for examination as potential domatia (Fig. 17), but after careful inspection, do not appear to offer habitat for mites or other animals. Specifically, there is not an obvious hollowed or sheltered area for them to utilize. Structures have been observed in *Meriania* Sw. and referred to as “scutums” or “swollen projections” (Fernandez-Hilario et al., 2023). Some minute petiolar protrusions in *Huberia* DC. (Fig. 17C) have been described as “domácias peciolares” [petiolar domatia] (Baumgratz, 1997, 2004). However, while a single invertebrate was observed near one (Fig. 18E), it is unclear whether or not structures

actually offer suitable habitat. Further, they often do not appear on specimens, and if they are present, may only appear on a few leaves. Extrafloral nectaries have been described in one species of Melastomataceae (Keeler et al., continuously updated), and it is possible that some of these structures may be serving other ecological roles. Thus, these scutums, swollen projections, and possible petiolar glands require further inspection.

Discussion

Summary

Leaf domatia across Melastomataceae are much more common than previously thought; 331 domatia-bearing species are catalogued here that, according to our literature review, have not before been recorded as possessing domatia. Melastomataceae now has the second most leaf domatia of all vascular plant families, behind only Rubiaceae (Myers et al., 2024). While second to Rubiaceae in number of species with small leaf domatia, Melastomaceae exhibits the greatest morphological diversity, with ten unique types described here. The inconsistency of published terms and definitions captured in this study represents the historical ontological discrepancies in domatia, and underpins the need for more unified definitions of domatia and their morphology. In addition, previous classifications have failed to capture the combination of invertebrate-conducive morphological characters that can be exhibited by a single domatium., e.g., recessed *and* marsupiform. Our classification allows for combinations of characters in order to more accurately describe domatium morphology. Before this survey, mites had been recorded in domatia of five species of Melastomataceae representing three types of domatia (*marsupiform, recessed,* and *tuft*). Now, we have evidence for mites in twelve species of Melastomataceae (Fig. 18), representing those three types of domatia, plus an additional type: *pit.* Lastly, our

acknowledgement of other leaf characters that could functionally serve as domatia sheds light on the gradient of leaf morphology that serves as suitable invertebrate habitat.

Limitations

We have chosen to accept a functional definition of domatia consistent with Lundström's original sense of the term, which should hold precedence over subsequent definitions. Thus, while mites and other invertebrates were observed in some types of domatia described here (Fig. 18), several structures will remain putative domatia until organisms have been observed in them. For example, although the *pinwheel* "domatia" in *Chalybea* Naudin represent unique structures that a) have been historically classified as domatia (Penneys & Judd, 2011; Wieser, 2025), and b) are consistent with invertebrate habitats offered by known domatia, no invertebrates have been observed dwelling in these structures. This is true for *revolute, petiolar*, and *volcano* domatia as well. Further, even if invertebrates are observed in one type of domatia of some species (e.g., *marsupiform*), this does not mean that all *marsupiform* structures across plants are functionally domatia. Confirmation of these structures as domatia will require species-level herbarium and field observations to record invertebrate presence and illustrate mutualism. Even then, the presence of invertebrates could be limited by a variety of factors that may be difficult to capture, like plant individual life span, seasonality, recent invertebrate extinction, etc.

Regardless, imaging and metabarcoding of herbarium specimens offer an exciting opportunity to elucidate the microbiomes and ecologies of plant species, especially over time (Heberling & Isaac, 2017; Bieker et al., 2020). Continued study of domatia, utilizing both historical herbarium collections and field observations, is crucial.

While our classification of domatia is, to our knowledge, inclusive of small leaf domatia found across vascular plants (Myers et al., 2024), there are a few dubiously synonymous examples of domatia that deserve mention. In Rubiaceae, for example, *cavern* and *crypt* domatia are described (Marcon & Bruniera, 2024). Upon inspection, these appear to fall under *pit* domatia within our classification, *cavern* representing a pit with a very small opening, and *crypt* representing a pit whose edges are slightly elevated from the leaf surface. Similarly, in Lauraceae, *dish* domatia have been described (Nishida et al., 2006), but these too appear to represent broadly open pits. In Marcgraviaceae, there are reports of very small *pit* domatia that occur not in the vein axils, but across the leaf surface (Brouwer & Clifford, 1990). If these are in fact domatia, they would not necessarily represent a distinct morphology from our classification, but they would represent a particularly unique developmental example. However, because of their size and placement, their function as domatia is apparently doubtful (Dressler, 2004). Anatomical comparison of domatia across plant families will shed light on these ambiguities.

Further Research

Given the most recent family-wide phylogeny of Melastomataceae (Penneys et al., 2022), mite domatia have evolved numerous times. The dataset presented here will allow for thorough investigation of the evolutionary patterns of domatia across the family. Namely, domatia have recently been linked to temperate climates: lower temperatures, less precipitation, and higher altitudes (Myers et al., 2024). It has been hypothesized that domatia are associated with dryer environments because they prevent mite desiccation (Walter, 1996). Investigating climatic associations with domatium presence and type within Melastomataceae, a primarily Tropical family, will challenge these global trends and have important implications for the conservation of

domatia-bearing plants and their invertebrate partners. Furthermore, while preliminary phylogenetic evidence points to convergent evolution of ant and mite domatia in Melastomataceae (Penneys et al., 2022), exploring the relatedness of these two domatia types could illuminate potentially homologous genes and/or developmental pathways.

Not only could the evolution of domatia be linked to climate on a macro scale, but expression of domatia may be affected by the environment too. We observed that 246 of the domatia-bearing species exhibit some level of variability in the presence of domatia. Further, we found conflicting information about domatium presence, absence, and/or type of domatium between vouchered specimens and type specimens, and/or vouchered specimens and the literature for 109 species. In some cases, these inconsistencies could represent a need for taxonomic revision between specimens, especially those for which findings differed between the literature, type specimens, and other herbarium specimens. However, variable expression between leaves, or between confirmed individuals of the same species, leads us to intriguing questions surrounding the development and plasticity of domatia. For example, in *Miconia sellowiana* Naudin, the variable size of domatia was linked to differences in habitat (Larcher de Carvalho et al., 2012), suggesting that environmental conditions may affect domatium development. It was proposed early on that the presence of mites could induce domatium development (Lundström, 1887). While no evidence exists to support this assertion, disentangling the interplay between genetic regulation and the environment, including mite presence and climatic conditions, will be an important step in understanding the evolution and development of domatia. Furthermore, multiple genes and complex pathways mediated by jasmonic acid and auxin were linked to variable tuft domatia development in *Vitis* L. (Ritter et

al., 2025). We hope the dataset presented here will offer exciting opportunities to ask similar questions about genetic regulation of domatia in Melastomataceae.

Although seemingly far less common and diverse than in Neotropical taxa, leaf domatia are also known to occur in several Paleotropical species of Melastomataceae. Their occurrence has been documented in *Dichaetanthera* Endl. (pit), *Dissotis* Benth. (pit) (Brouwer & Clifford, 1990), *Gravesia* Naudin (unspecified) (Almeda & Ranarivelo, 2019), *Heteroblemma* (Blume) Cámara-Leret, Ridd.-Num. & Veldkamp (pouch) (Cámara-Leret et al., 2013), and *Rousseauxia* DC. (unspecified) (Gregory, 1990). Again, the use of *pouch* is ambiguous here, and underpins the importance of a more comprehensive terminology. Further, a comparison of domatia morphology and function between the Neo and Paleotropics could clarify global trends across the family.

Conclusion

This study is the first in-depth survey of leaf domatia across Melastomataceae. Utilizing 3,581 herbarium specimens and 83 publications, we reconcile 50 previously used terms into ten clearly defined categories. Not only will a unified domatia classification eliminate confusion, utilizing simple and universal terminology will lead to improved species identification, as well as clear species description and delimitation. While small, leaf domatia represent an underutilized character for taxonomy and identification, particularly in sterile specimens. Because Melastomataceae harbors the most impressive diversity of these structures in all vascular plant families, to our knowledge, this classification is inclusive of all small leaf domatium morphologies in other families (Myers et al., 2024), and thus, can be employed across vascular plants.

Hundreds of presence points (331) and thousands of absence points (2,121) for species not previously recorded in the reviewed literature are included here, expanding our understanding of the prevalence and diversity of domatia both in Melastomataceae and across vascular plants. These data lay the groundwork for exciting process-level questions about the ecology and evolution of domatia.

The other leaf characters recorded here serve as another interesting point of investigation. We have discussed the gradient between characters that create a suitable hiding place for mites and more obvious structures historically considered domatia (e.g., indumentum vs. tuft domatium). We wonder, where should we draw the line around what is a domatium, if there is one, and what are the implications of this line? Closer investigation of these borderline leaf characters, via a combination of anatomical study, microscopy, and DNA metabarcoding, will shed light on these questions.

This work highlights the power of natural history collections and continues to expand our understanding of the "extended specimen" (Webster, 2017). Not only are herbarium specimens a goldmine for interesting morphological studies of plant traits, but they also clearly harbor immense amounts of biological diversity beyond that of the plant itself. Not one of the thousands of specimens examined here lacked evidence of some invertebrate, fungi, or other living creature. The depth of ecological data held in a single herbarium specimen, and the questions that could be asked with this data, are quite frankly, overwhelming.

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Declarations

***Competing Interests*.** The authors have no competing interests to declare that are relevant to the content of this article.

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Author's contributions. KS and FM designed the study. FM advised on domatia background and study objectives. MM, NM, TD and KS conducted the herbarium survey. FM, KS, MM, NM, and TD contributed equally to imaging, as well as the synthesis of domatia definitions. KS did the writing and figure preparation. All authors contributed to editing and final draft feedback.

Data availability. The data supporting the findings of this study are available in Appendix 1.

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Figure

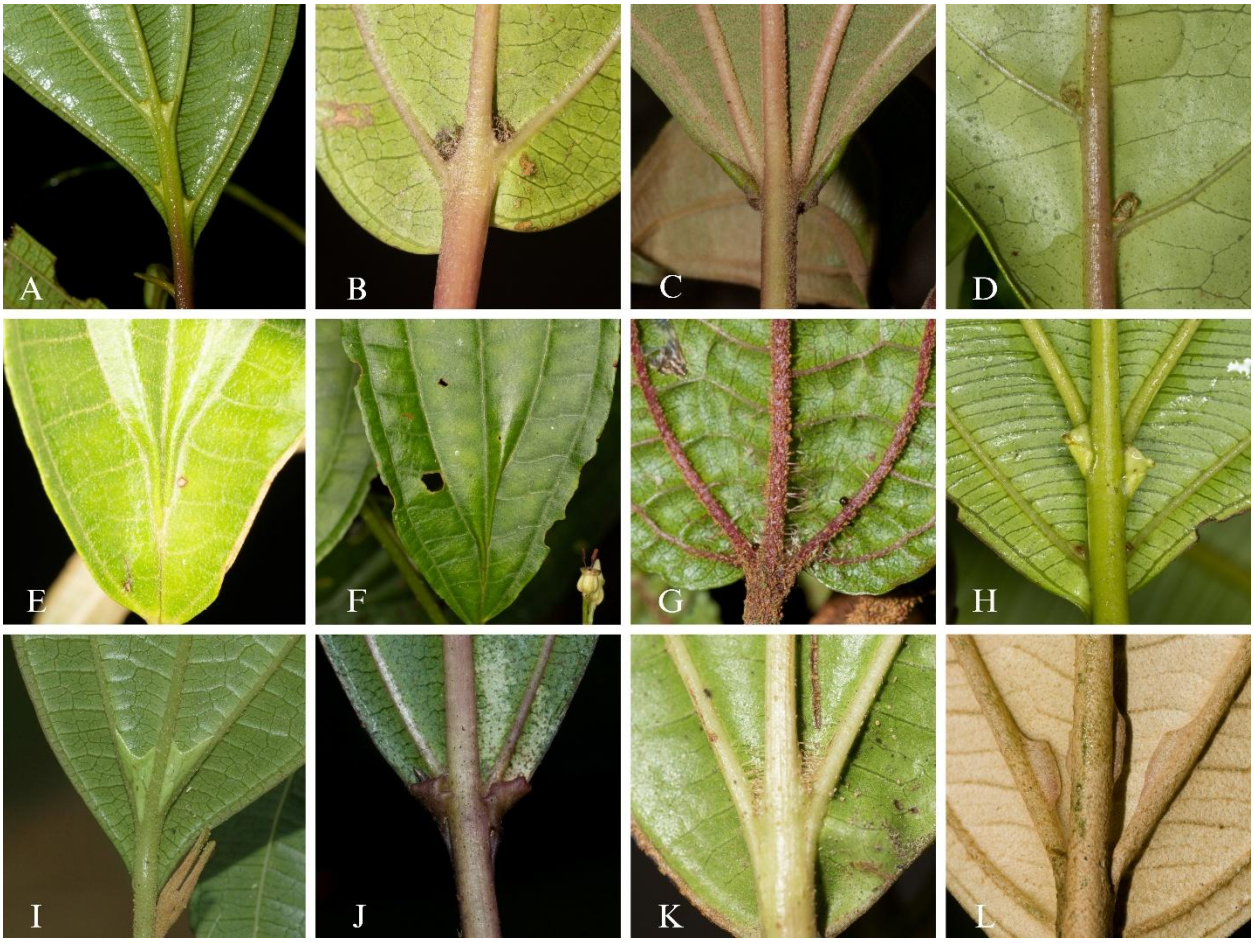


Fig. 1. Diversity of small leaf domatia in Melastomataceae. **A.** *Miconia ecuadorensis* [FAM 1825] **B.** *Miconia sp.* [FAM 2646] **C.** *Axinaea macrophylla* [FAM 1957] **D.** *Miconia glabrifolia* [FAM 2251] **E.** *Miconia* aff. *neomicrantha* [FAM 3458] **F.** *Miconia* cf. *neomicrantha* [FAM 3463] **G.** *Miconia lachnoclada* [FAM 1946] **H.** *Blakea henripittieri* [FAM 3320] **I.** *Miconia doriana* [Goldenberg 829] **J.** *Meriania cuzcoana* [FAM 1908] **K.** *Miconia brevis* [FAM 2662] **L.** *Chalybea macrocarpa* [NA]. (all photos by FAM)

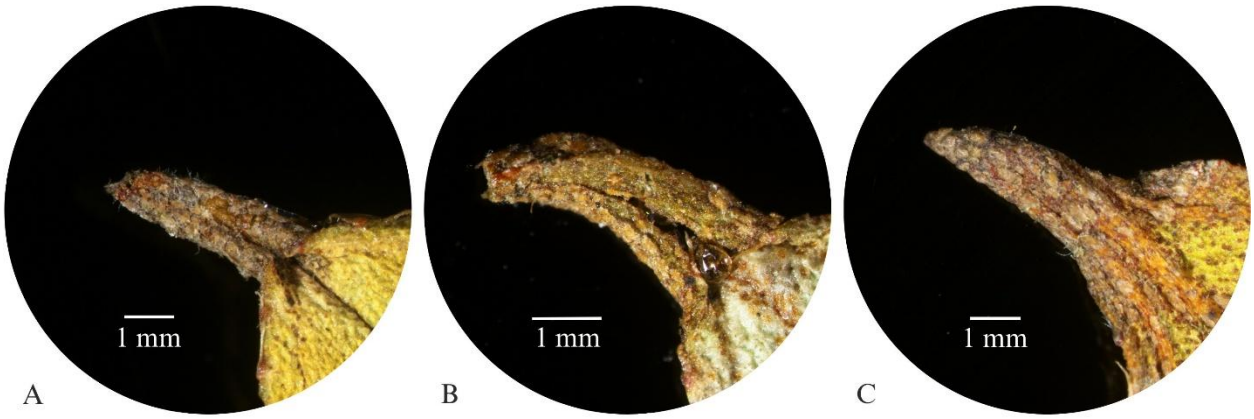


Fig. 2. Apical. **A.** *Henriettea uniflora* adaxial view NY-03236018 [KS]. **B.** *Henriettea uniflora* adaxial view NY-03236018 [KS]. **C.** *Henriettea uniflora* abaxial view NY-03236018 [KS].

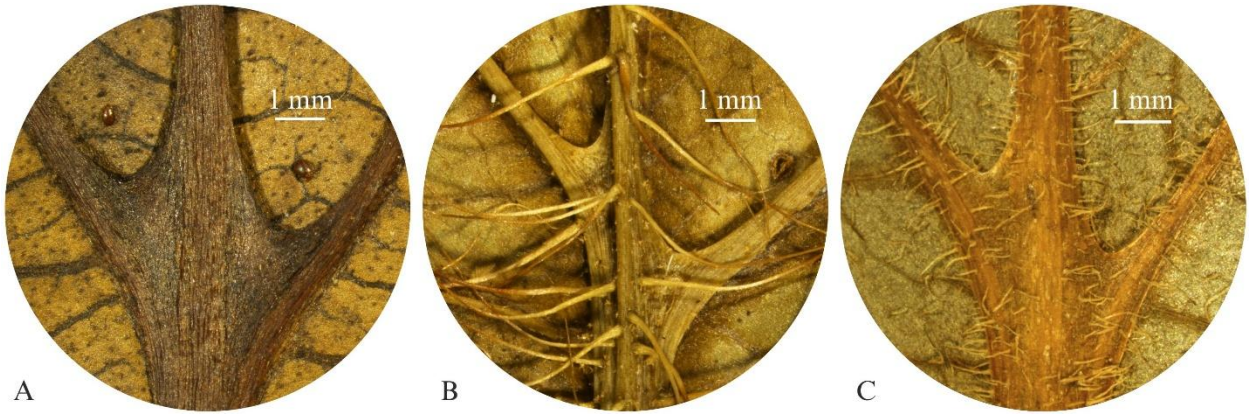


Fig. 3. Marsupiform. **A.** *Miconia rupestris* NY-1653859 [KS]. **B.** *Miconia laevifolia* NY-01289480 [KS]. **C.** *Aciotis viscida* NY-01254025 [KS].

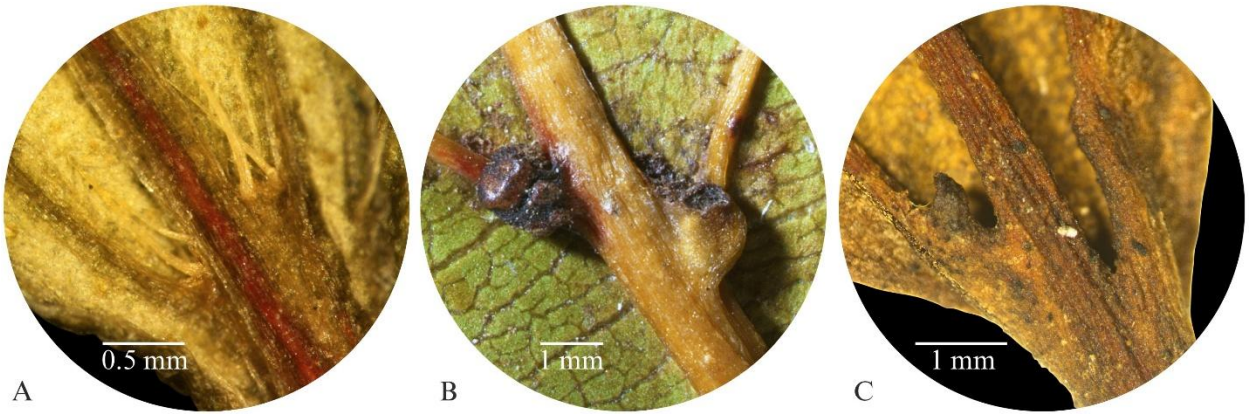


Fig. 4. Marsupiform subtypes. **A.** ciliate *Monochaetum uribei* NY-03108598 [KS]. **B.** inflated *Miconia microdictya* NY-04314035 [KS]. **C.** fissured *Huberia weberbaueriana* NY-02678623 [KS].

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Fig. 5. Petiolar. **A.** *Miconia argentea* NY-02518271 [KS]. **B.** *Blakea chlorantha* NY-02685185 [KS]. **C.** *Blakea austin-smithii* NY-03144561 [KS].

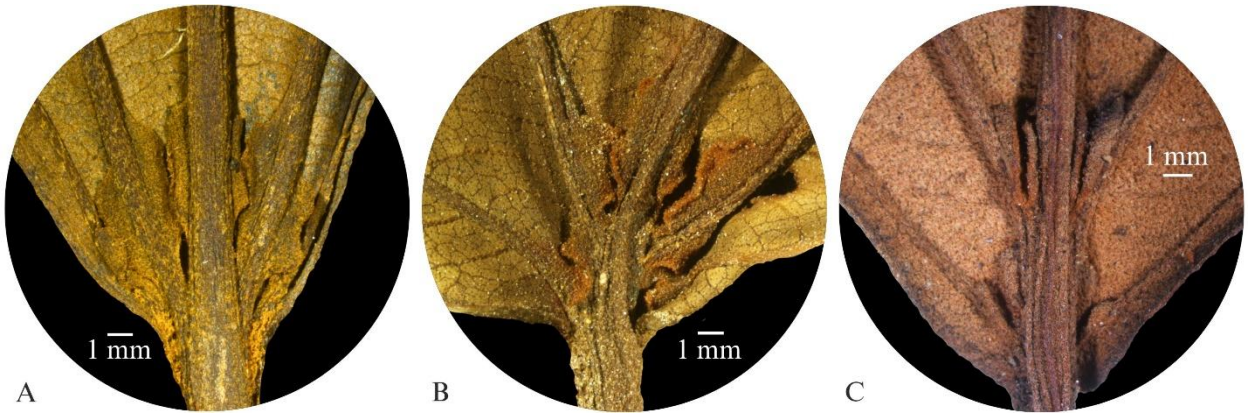


Fig. 6. Pinwheel. **A.** *Chalybea brevipedunculata* NY-03785504 [KS]. **B.** *Chalybea ecuadorensis* NY-03166655 [KS]. **C.** *Chalybea peruviana* NY-03784725 [MM].

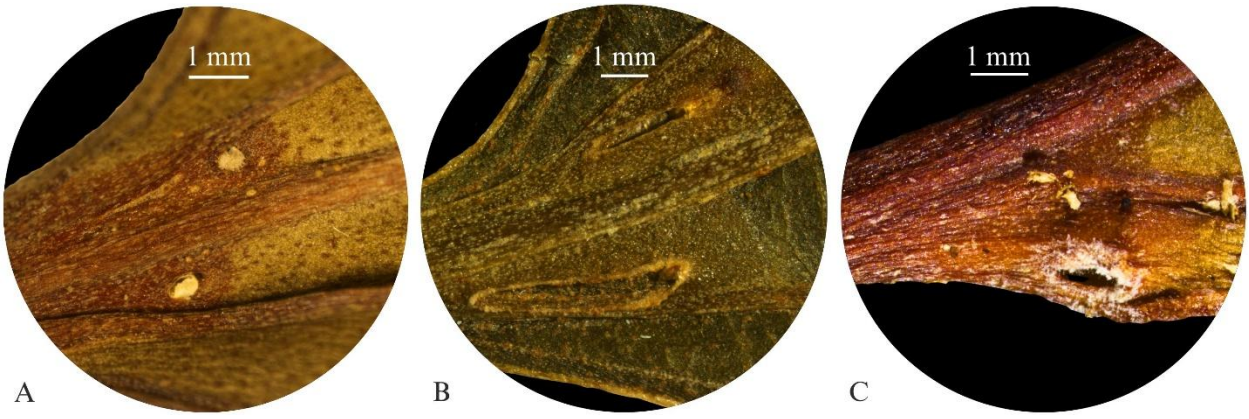


Fig. 7. Pit. **A.** *Blakea pulverulenta* NY-02685358 [NM]. **B.** *Blakea gracilis* NY-02684884 [TD]. **C.** Marginal pit *Blakea laevigata* NY-03144769 [KS].

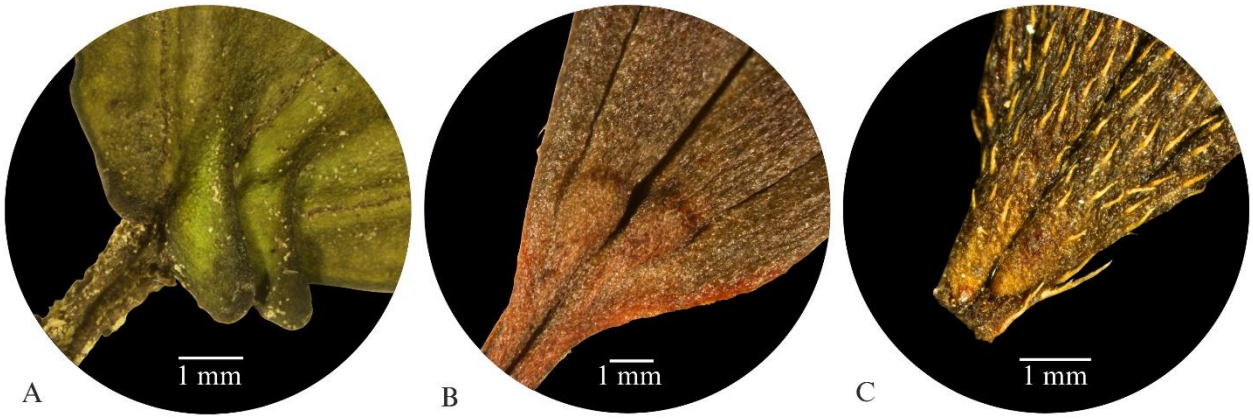


Fig. 8. Recessed. **A.** *Meriania purpurea* NY-01264453 [KS]. **B.** *Blakea inflata* NY-03676587 [KS]. **C.** *Brachyotum jamesonii* NY-02514253 [KS].

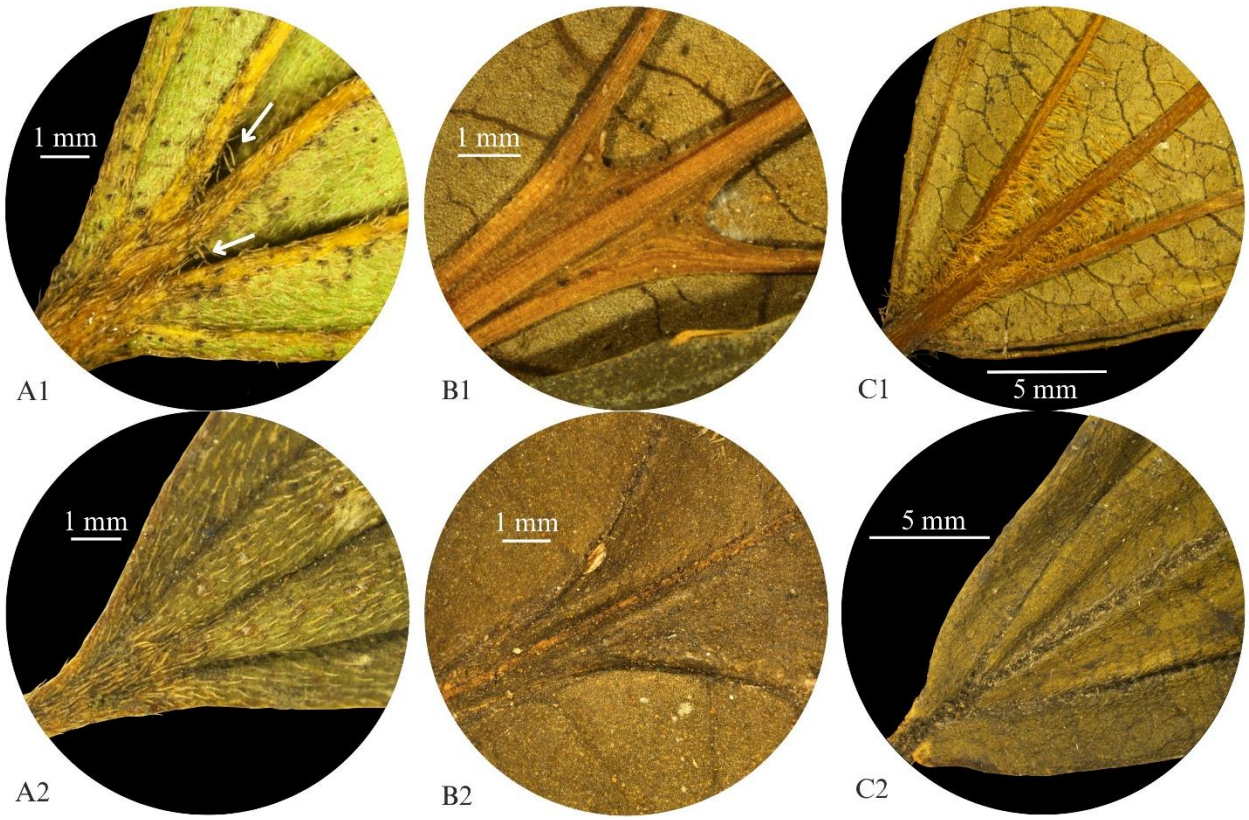


Fig. 9. Recessed subtypes. **A.** recessed venous *Pleroma mutabile* NY-02514375 [KS] abaxial (**A1)** and adaxial (**A2)** views. **B.** recessed marsupiform *Miconia ciliolata* NY-04297785 [KS] abaxial (**B1**) and adaxial (**B2**) views. **C.** Recessed tuft *Miconia chrysocoma* NY-1599090 [KS] abaxial (**C1)** and adaxial (**C2**) views.

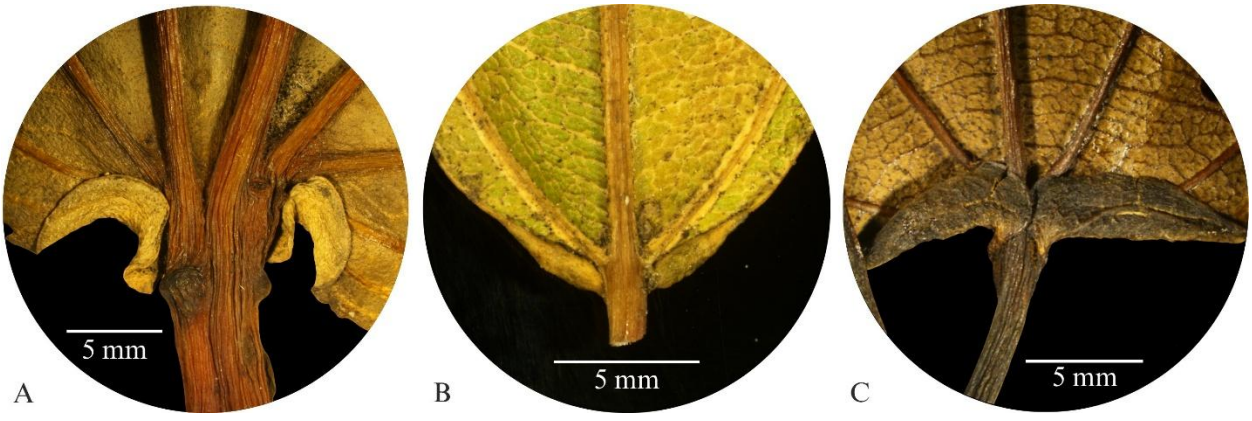


Fig. 10. Revolute. **A.** *Meriania nobilis* NY-02500157 [KS]. **B.** *Miconia tricostata* NY-04314009 [KS]. **C.** *Axinaea scutigera* NY-03677031 [TD].

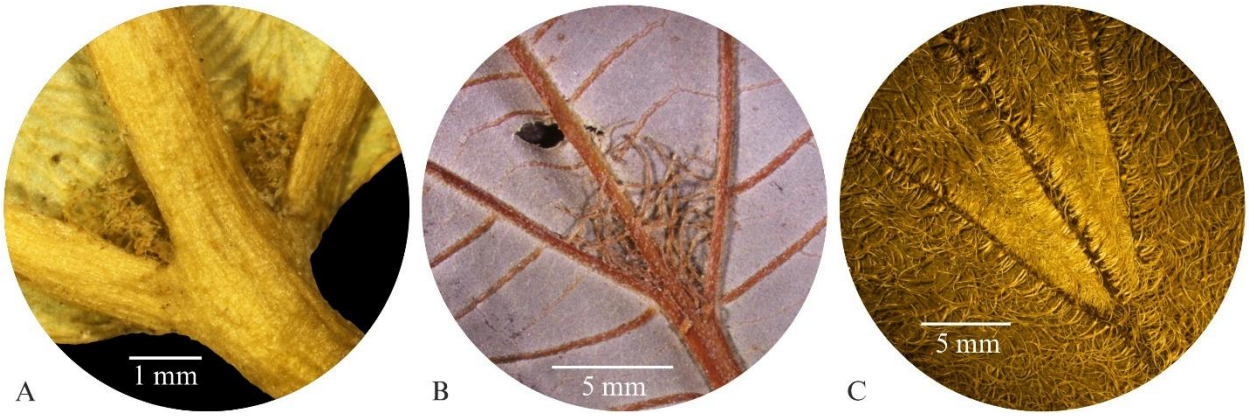


Fig. 11. Tuft. **A.** *Meriania albiflora* NY-01264434 [KS]. **B.** *Graffenrieda obliqua* NY-2464799 [FM]. **C.** *Miconia glomeruliflora* NY-01100730 [TD].

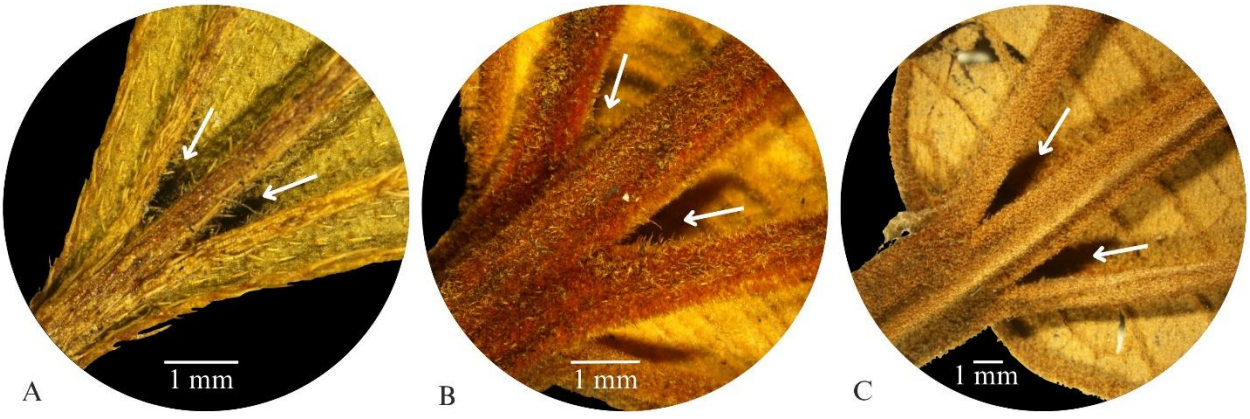


Fig. 12. Venous. **A.** *Pleroma raddianium* NY-00558366 [KS]. **B.** *Miconia superba* NY-03460205 [KS]. **C.** *Miconia rondoniensis* NY-00987409 [KS].

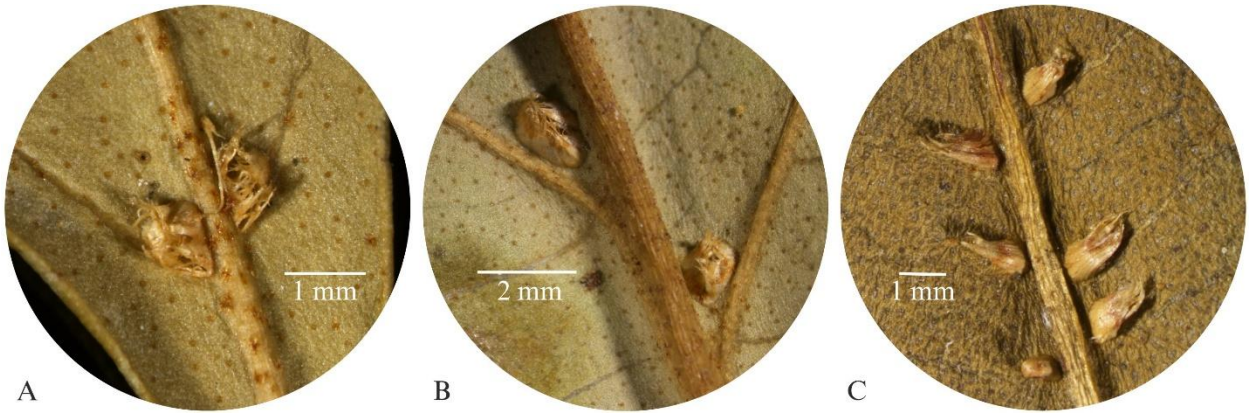


Fig. 13. Volcano. **A.** *Miconia microphylla* NY-1636991 [KS]. **B.** *Miconia glabrifolia* NY-01164162 [MM]. **C.** *Miconia vulcanidomatia* NY-01129989 [KS].

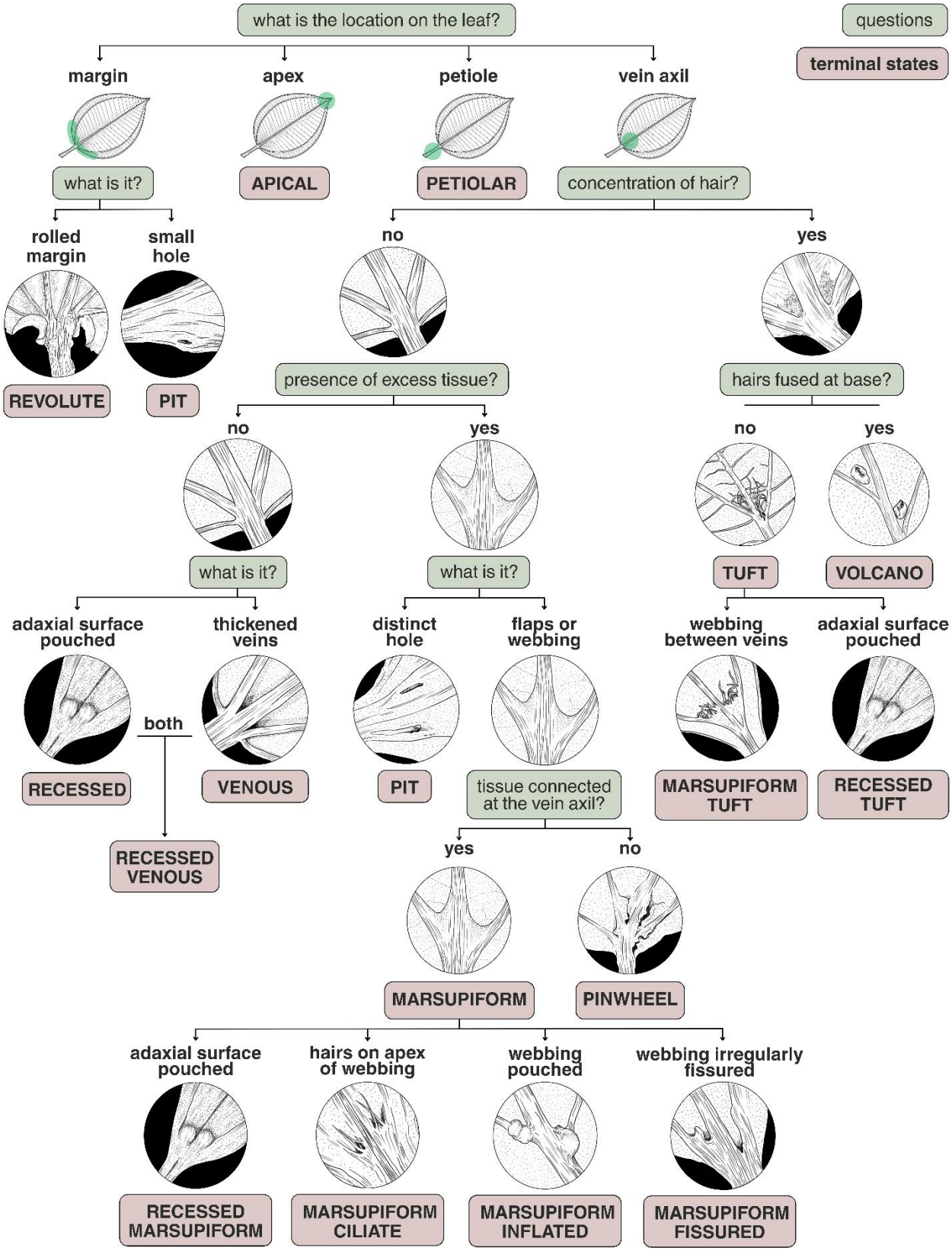

what is the location on the leaf?
questions
terminal states
margin
apex
petiole
vein axil
what is it?
APICAL
PETIOLAR
concentration of hair?
rolled margin
small hole
no
yes
REVOLUTE
PIT
presence of excess tissue?
hairs fused at base?
no
yes
no
yes
what is it?
what is it?
TUFT
VOLCANO
adaxial surface pouched
thickened veins
distinct hole
flaps or webbing
webbing between veins
adaxial surface pouched
both
RECESSED
VENOUS
PIT
tissue connected at the vein axil?
MARSUPIFORM TUFT
RECESSED TUFT
RECESSED VENOUS
yes
no
MARSUPIFORM
PINWHEEL
adaxial surface pouched
hairs on apex of webbing
webbing pouched
webbing irregularly fissured
RECESSED MARSUPIFORM
MARSUPIFORM CILIATE
MARSUPIFORM INFLATED
MARSUPIFORM FISSURED

Fig. 14: Flow chart to aid in classification of domatia. If there are structures in multiple locations on the leaf, the user should run through the chart multiple times. For example, although rare, some species might have marsupiform morphology in the vein axil, and revolute morphology along the margin. Illustrations by Mary Quinlan.

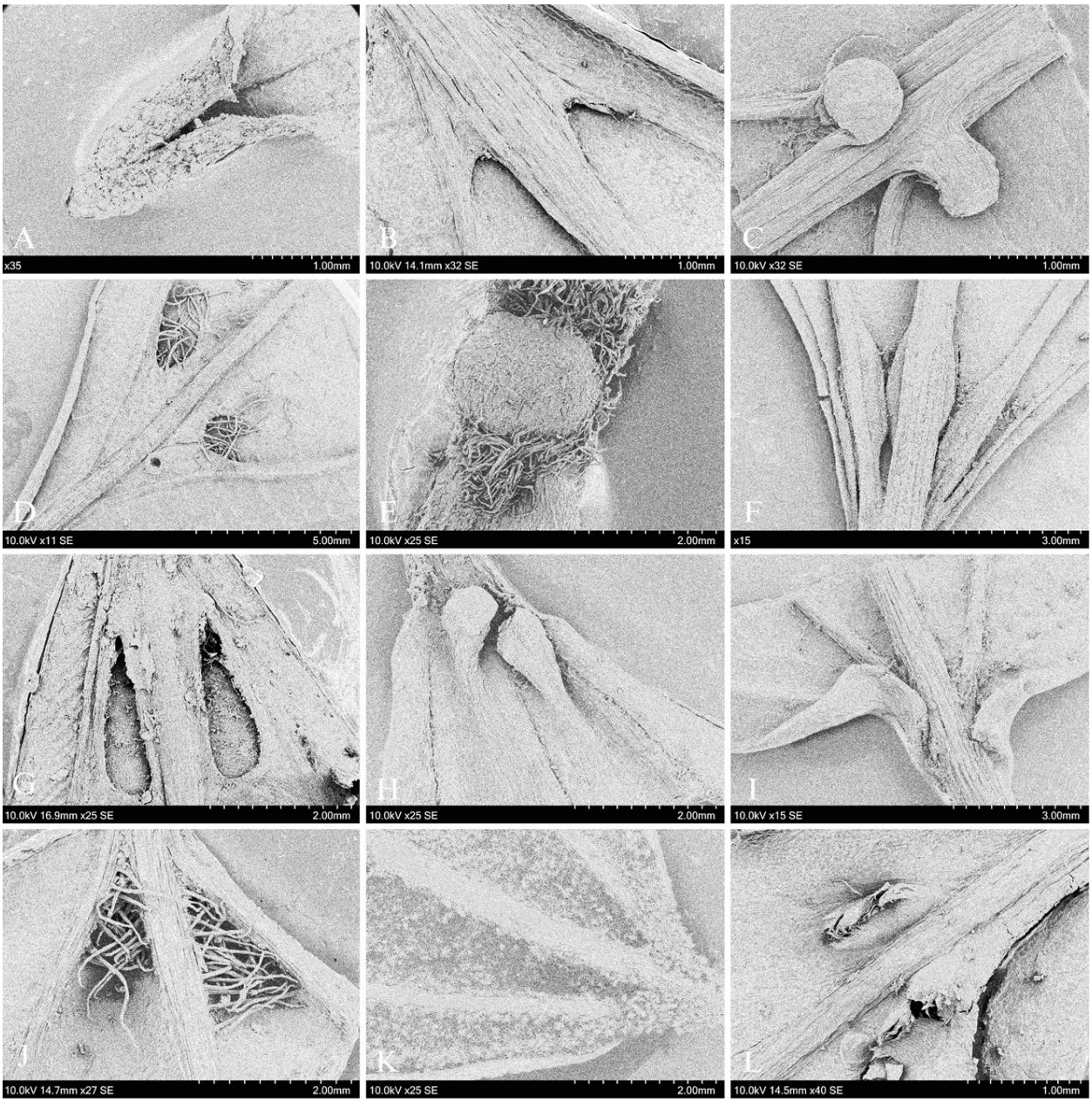


Fig. 15. SEM images of domatia types. **A.** Apical (adaxial) *Henriettea uniflora* NY-03236018 [TD]. **B.** Marsupiform *Miconia ligustrina* NY-3272624 [MM]. **C.** Marsupiform inflated *Miconia microdictya* NY-04314035 [TD]. **D.** Marsupiform tuft *Miconia biperulifera* NY-03215158 [TD]. **E.** Petiolar *Blakea chlorantha* NY-02685185 [TD]. **F.** Pinwheel *Chalybea brevipedunculata* FernandezHilario3215 [TD]. **G.** Pit *Blakea pauciflora* NY-02684949 [NM]. **H.** Recessed (adaxial) *Meriania purpurea* NY-01264453 [TD]. **I.** Revolute *Axinaea nitida* NY-02450445 [TD]. **J.** Tuft *Miconia schnellii* NY-01421386 [MM]. **K.** Venous *Miconia aspergillaris* NY-3241591 [TD]. **L.** Volcano *Miconia vulcanidomatia* NY-01129962 [MM].

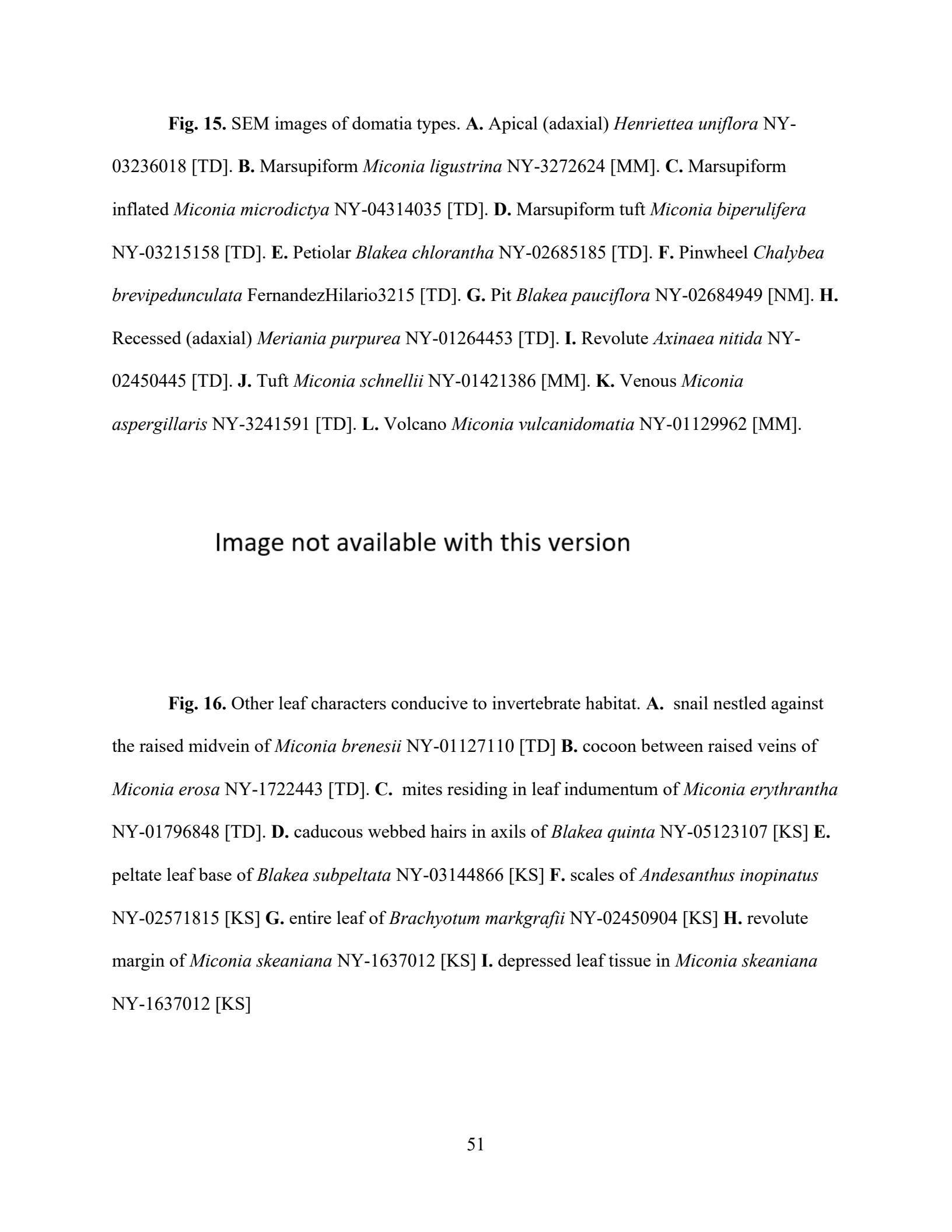


Fig. 16. Other leaf characters conducive to invertebrate habitat. **A.** snail nestled against the raised midvein of *Miconia brenesii* NY-01127110 [TD] **B.** cocoon between raised veins of *Miconia erosa* NY-1722443 [TD]. **C.** mites residing in leaf indumentum of *Miconia erythrantha* NY-01796848 [TD]. **D.** caducous webbed hairs in axils of *Blakea quinta* NY-05123107 [KS] **E.** peltate leaf base of *Blakea subpeltata* NY-03144866 [KS] **F.** scales of *Andesanthus inopinatus* NY-02571815 [KS] **G.** entire leaf of *Brachyotum markgrafii* NY-02450904 [KS] **H.** revolute margin of *Miconia skeaniana* NY-1637012 [KS] **I.** depressed leaf tissue in *Miconia skeaniana* NY-1637012 [KS]

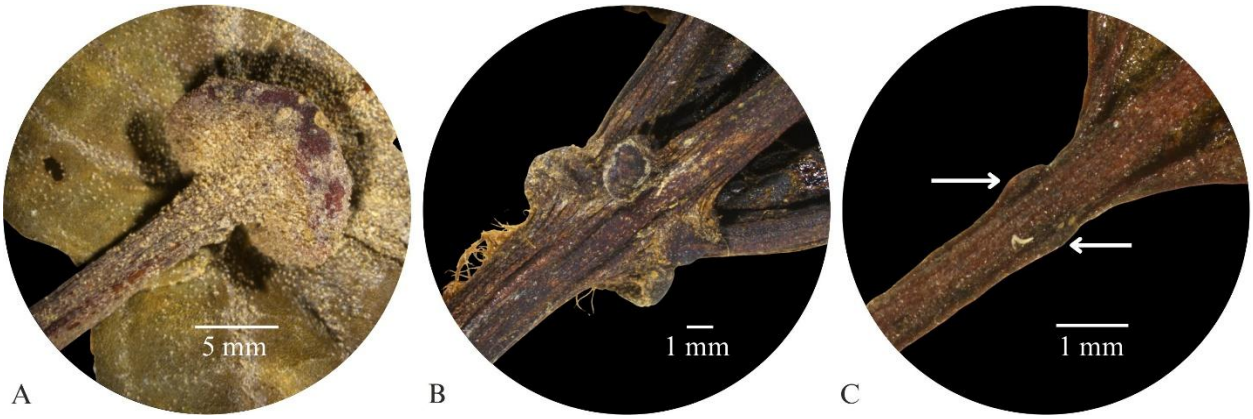


Fig. 17. Structures resembling domatia but requiring additional study. **A.** thickened petiole apex of *Miconia clypeata* NY-03108535 [KS]. **B.** thickened glands on *Miconia rodriguezii* NY-01165286 [KS]. **C.** protruding tissue on petiole of *Huberia peruviana* NY-01164965 [KS].

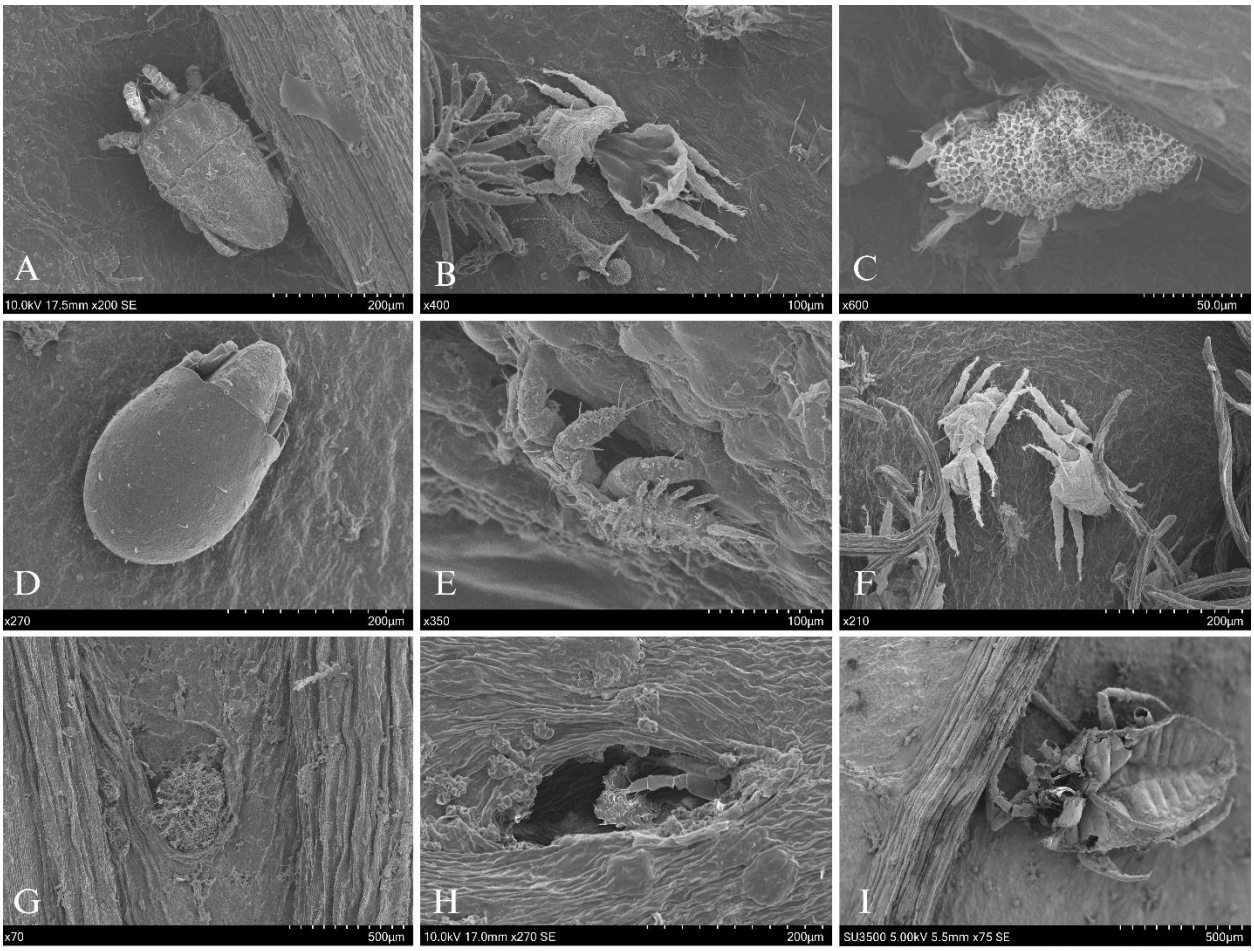


Fig. 18. Invertebrates found on herbarium specimens. **A.** Tydeidae near marsupiform domatium of *Miconia* cf. *flavescens* NY-03376556 [NM]. **B.** exuviae of Tydeidae in tuft domatium of *Miconia mexicana* NY-03216241 [TD]. **C.** *Lorryia* in recessed marsupiform domatium of *Brachyotum johannes-julii* NY-02424426 [TD]. **D.** Oribatida near marsupiform domatium of *Miconia rupestris* NY-1653859 [TD]. **E.** unknown mite (possibly hiding beneath the exuviae of another arthropod) near petiolar structures of *Huberia peruviana* NY-01164965 [TD]. **F.** exuviae of Tydeidae on hairy leaf surface of *Miconia erythrantha* NY-01796848 [TD]. **G.** unknown structure in pit domatium of *Blakea pulverulenta* NY-02685358 [TD]. **H.** Oribatida in pit

domatium of *Blakea parvifolia* NY-Almeda5898 [NM]. **I.** exuviae of Hemiptera near marsupiform tuft domatium of *Miconia castillensis* NY-02684799 [TD]. Determinations by Heather Proctor and David Evans Walter.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Appendix1.xlsx
- Table1.docx