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Ecology and Evolution of Domatia in Pyxidantheae (Melastomataceae)

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Abstract

Acarodomatia, sometimes also called leaf domatia, have been observed in over 2500 plant species and can house mites and other small arthropods as potential mutualists. Acarodomatia usually sit on the abaxial side of a leaf, in the axils of leaf veins and consist of a small cavity obstructed by hairs, veins or pocket-like tissue. Mites can be beneficial to domatia-bearing plants by feeding on fungi, bacteria and lichen growing on its leaves or predating on small herbivores. In turn, the plants provide shelter for the mites to moult or lay their eggs. Since research on acarodomatia primarily focuses on agriculturally significant plants in temperate regions, there are few studies on the mutualism between tropical plants with domatia and mites.

To address this research gap, I studied the domatia of the neotropical tribe Pyxidantheae (Melastomataceae), comprising over 200 species in the genera *Blakea* P.Browne and *Chalybea* Naudin, which shows great morphological diversity in domatia types, despite growing in relatively similar ecosystems, moist rainforest. To explore the ecology and evolution of domatia in Pyxidantheae I assessed domatia presence and type of 150 species with specimens from online repositories and five herbaria. To understand the evolutionary background, I performed ancestral character estimations and stochastic character mappings with presence/absence and the different types of domatia. I tested for a correlation between climatic conditions, temperature, precipitation and elevation, and the presence of domatia with phylogenetic ANOVAs. I conducted fieldwork in Colombia for two months, recording domatia presence and collecting inhabitants from leaves of eight *Blakea* species across seven sites. I analysed diversity using the Shannon index based on my arthropod morphotypes. To assess microclimatic effects, I recorded leaf age and sun exposure in five individuals of *Blakea quadrangularis*.

By assessing herbarium specimens, I added 26 more species to the 30 species previously described to have domatia and found that domatia have multiple evolutionary origins in Pyxidantheae. Some types of domatia, like hair tufts and marsupiform pockets, evolved multiple times convergently in the tribe, while others are restricted to certain clades. I found no significant correlation between climatic conditions and domatia presence. However, I did find evidence that the microclimate, like sun exposure, may influence if a leaf develops domatia or not. In my investigation young leaves had domatia more often than old leaves. Since I only found unidentifiable eggs in *Blakea podagrica* Triana and adult arthropods in other species, it seems that seasonality not only influences domatia development but also the developmental stage the inhabitants are in.

In my thesis, I combined macroevolutionary with macro- and microecological methods to unveil processes involved in the evolution and ecology of domatia. With this work, I provide the basis for further investigations to understand the ecology of tropical mite-plant mutualisms mediated by domatia and make concrete suggestions on how to expand upon my findings.

Abstract (Deutsch)

Acarodomatien, auch Blattdomatien genannt, wurden bei über 2500 Pflanzenarten beobachtet und können Milben und andere kleine Arthropoden als potentielle Mutualisten beherbergen. Acarodomatien befinden sich meistens auf der abaxialen Seite eines Blatts, in den Achseln der Blattnerven und bestehen aus einem kleinen Hohlraum verdeckt durch Haare, Blattnerven oder taschenartigem Gewebe. Milben können für Pflanzen mit Domatien nützlich sein, indem sie Pilze, Bakterien und Flechten, die auf Blättern wachsen, fressen oder indem sie kleine Herbivoren jagen. Die Pflanzen wiederum bieten den Milben Unterschlupf, um sich zu häuten oder Eier abzulegen. Da sich Forschung zu Acarodomatien meist auf landwirtschaftlich bedeutsame Pflanzen in temperaten Regionen konzentriert, gibt es wenige Studien zum Mutualismus zwischen tropischen Pflanzen mit Domatien und Milben.

Um diese Forschungslücke zu schließen, untersuchte ich die Domatien der neotropischen Tribus Pyxidantheae (Melastomataceae), bestehend aus über 200 Arten in den Gattungen *Blakea* P.Browne und *Chalybea* Naudin, die trotz ihres Vorkommens in relativ ähnlichen Ökosystemen, feuchter Regenwald, eine große morphologische Vielfalt an Domatien-Typen zeigen. Um die Ökologie und Evolution von Domatien in Pyxidantheae zu erforschen, evaluierte ich Domatienpräsenz und -typ bei 150 Arten mit Belegen aus Online-Archiven und fünf Herbarien. Um den evolutionären Hintergrund zu verstehen, führte ich „ancestral character estimations" und „stochastic character mapping", mit Präsenz/Absenz und mit den verschiedenen Domatientypen, durch. Ich prüfte den Zusammenhang zwischen Klimabedingungen, Temperatur, Niederschlag und Höhenlage, und Domatienpräsenz mit phylogenetischen ANOVAs. Ich führte Feldarbeit in Kolumbien für zwei Monate durch, in der ich Domatienpräsenz dokumentiert und Bewohner der Blätter von acht *Blakea*-Arten an sieben Standorten gesammelt habe. Ich analysierte Diversität mit dem Shannon Index basierend auf meinen Arthropoden-Morphotypen. Um mikroklimatische Effekten zu evaluieren, erfasste ich Blattalter und Sonnenexposition bei fünf Individuen von *Blakea quadrangularis*.

Durch die Auswertung der Herbarbelege, konnte ich 26 weitere Arten zu den zuvor 30 beschriebenen Arten mit Domatien hinzufügen und stellte fest, dass Domatien in Pyxidantheae mehrfach unabhängig evolviert sind. Manche Domatientypen, wie Haarbüschel oder taschenförmige Domatien, entwickelten sich mehrmals konvergent in der Tribus, während andere auf bestimmte Kladen beschränkt sind. Ich fand keine signifikante Korrelation zwischen klimatischen Bedingungen und Domatienpräsenz. Allerdings fand ich Hinweise darauf, dass Mikroklima, wie Sonnenexposition, beeinflussen könnte ob ein Blatt Domatien ausbildet oder nicht. In meiner Investigation hatten junge Blätter öfter Domatien als alte Blätter. Da ich nur unidentifizierbare Eier in *Blakea podagrica* Triana und erwachsene Arthropoden in anderen Arten gefunden habe, könnte es darauf hinweisen, dass Saisonalität nicht nur die Domatienentwicklung, sondern auch die Entwicklungsstufe in der sich Bewohner gerade befinden, beeinflusst.

In meiner Masterarbeit habe ich makroevolutive mit makro- und mikroökologischen Methoden kombiniert um Prozesse zu enthüllen die in der Evolution und Ökologie von Domatien involviert sind. Mit dieser Arbeit liefere ich die Basis für zukünftige Investigationen um die Ökologie von tropischen Milben-Pflanzen Mutualismen mediiert durch Domatien zu verstehen und schlage konkret vor wie man meine Erkenntnisse vertiefen könnte.

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Introduction

Since plants are often affected by herbivory, epiphytes and pathogens they have evolved a variety of strategies to cope with these challenges. Many plants use chemical or mechanical defences, such as producing specialised metabolites that can be harmful to the herbivore or growing trichomes as a physical barrier (Fürstenberg-Hägg et al., 2013). Another strategy involves incorporating mutualistic partners that defend the plant in exchange for food, shelter or both. Domatia, the structures formed by plants to house (from "domus", Latin for house) and sometimes feed arthropod symbionts, are widely spread in angiosperms and can be built by various vegetative parts of a plant (Chomicki et al., 2024; Myers et al., 2024). The arthropods, mostly ants and/or mites, can inhabit cavities of the stem, hollow and enlarged roots or specialised leaves with hairs or protective tissue shielding the small tenants (Chomicki et al., 2024). In turn, the arthropods defend their host plants. Wounds caused by fungi, lichen, bacteria and animals, feeding on the leaf or from growing into plant tissue, can be entry points for pathogens damaging the plant further (Coley et al., 1993). In plants that form domatia, ants usually attack herbivorous intruders, while mites feed on the epiphylls, small herbivores and pathogens (Chomicki et al., 2024). While Chomicki & Renner (2015) estimated that over a thousand species provide domatia for ants, Myers et al. (2024) identified 2514 plant species that grow domatia for mites.

In this study, I am focusing on domatia that house mites, called acarodomatia. The mutualism between mites living in them and plants providing them was already proposed in 1887 by Lundström. Mite use of domatia has been documented in a wide range of plants across the world (English-Loeb et al., 2002; Pemberton & Turner, 1989; Richards & Coley, 2012; Romero & Benson, 2004; Walter, 1996). Mites use leaf domatia to lay their eggs sheltered from harsh climatic conditions and predation but also to moult, leaving their exoskeleton behind (Walter, 1996). The majority of mites found in domatia belong to primarily predacious families Phytoseiidae, Stigmaeidae and Tydeidae and can be beneficial to the plant by predating on small herbivores such as other mites or thrips (English-Loeb et al., 2002; Nishida et al., 2005). Other mites that have been found in leaf domatia and belong to the families of Tenuipalpidae and Eriophyidae can be harmful to plants since they feed on them (Pemberton & Turner, 1989). Romero & Benson (2004) performed one of the few studies in the tropics on acarodomatia and found mites belonging to predatory mite families Phytoseiidae, Stigmataeidae and Ascidae, fungivorous mites of the families Tarsonemidae and Winterschmidtiidae and the order Oribatida and phytophagous mites from Eriophyidae. These three categories, predatory, fungivorous and phytophagous, are used to infer the relationship between the mites and the plant bearing leaf domatia. While phytophagous mites can harm plants and pose a problem in agriculture, fungivorous and predatory mites are known to improve plant health (Agrawal et al., 2000). For example, predatory mites are used in agriculture as crop protection because they feed on pests such as spider mites (Tetranychidae), thrips and whiteflies (Knapp et al., 2018). Other studies show that planting cultivars of grapes that grow domatia or banker plants with domatia can improve overall crop health (English-Loeb et al., 2002; Parolin et al., 2015). The mites living in the domatia kept populations of predatory and fungivorous mites in check, and foraged on mildew.

Acarodomatia can take many forms but are usually located in the vein axils on the abaxial side of a leaf and the tissue growing in these axils defines the type of domatia (Chomicki et al., 2024). Common forms of leaf domatia are hair tuft, pit and pocket domatia and always feature a cavity varying in volume (Myers et al., 2024). In hair tuft domatia, trichomes grow densely packed where leaf veins diverge and often disguise a small cavity (Figure 1, no. 1) (Chomicki et al., 2024). In pit domatia, the cavity is hidden by tissue growing around it and can only be accessed by a small pore (Figure 1, no. 4) (Myers et al., 2024). Pocket domatia are cavities made from tissue growing between the veins (Figure 1, no. 2) (O'Dowd & Willson, 1989).

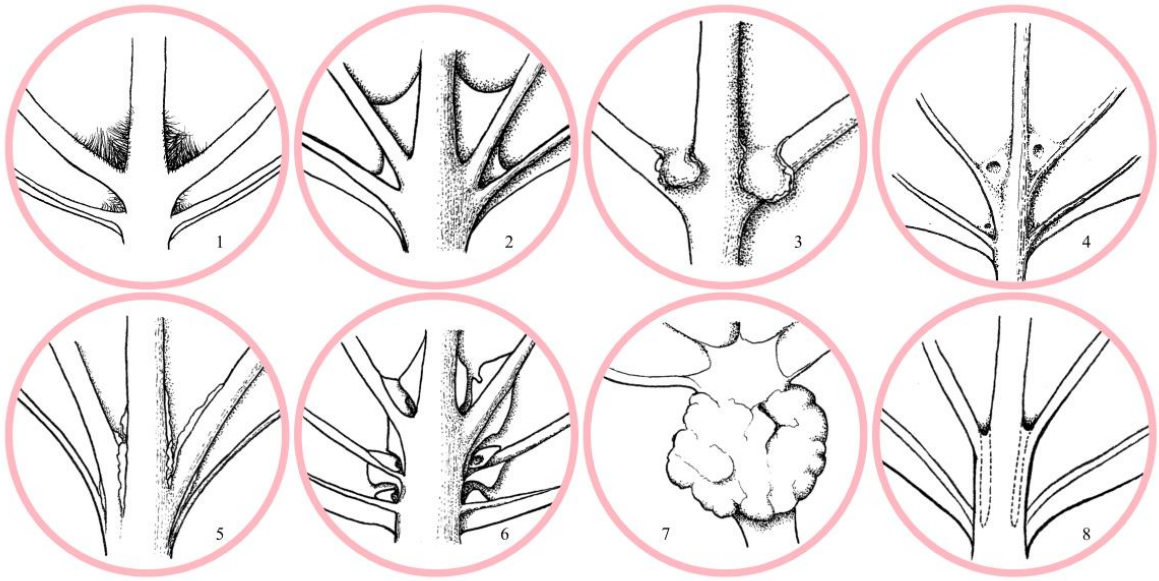

Figure 1. Drawings of domatia types in Pyxidantheae; 1=hair tuft domatia, 2=marsupiform pocket, 3=open pockets, 4=recessed pits, 5=lateral laminae, 6=pinwheel domatia, 7=petiolar flap, 8=coalesced veins.

Research on acarodomatia generally focuses on agriculturally significant topics, especially regarding pest control in European crops (English-Loeb et al., 2002; Parolin et al., 2011, 2015). Most plants bearing acarodomatia grow in temperate to dry ecosystems, while ant domatia are dominant in the tropics (Myers et al., 2024). According to Myers et al. (2024), hair tuft domatia are associated with dry climates and protect mites and their eggs from desiccation while pit domatia are found more often at lower latitude i.e. in the tropics, potentially protecting mites and their eggs from heavy rainfall and predators. Despite these differences in form and distribution, their function remains largely similar: domatia are a space for mites to lay eggs, moult and hide (Pemberton & Turner, 1989). While more plants with acarodomatia are found in drier regions, there is also a number of tropically distributed plants with domatia (Myers et al., 2024). With continuous growing seasons and high productivity in tropical habitats, a plant's need for protection against leaves being overgrown and damaged by epiphylls like fungi, lichen or algae is high (Coley et al., 1993). Plants are also subject to high herbivore pressure in the tropics (Salazar & Marquis, 2012). Due to this combination of climatic conditions and biotic influences, having domatia might be an advantage for tropical plants too.

Due to the limited knowledge about acarodomatia in the tropics, I selected the neotropically distributed tribe Pyxidantheae (formerly known as Blakeeae) as my study system. Their distribution centre is Colombia with 79 described species occurring there (Penneys & Almeda, 2022). The tribe is made up of two genera, *Blakea* P.Browne and *Chalybea* Naudin and includes over 200 species (Penneys & Almeda, 2022). Plants of this tribe grow at different elevations ranging from sea level to 3500 meters but the ecosystems in which they are found most often are mountainous rainforests and cloud forests (Penneys & Almeda, 2022). Most Pyxidantheae species are hemiepiphytes, with some exceptions, such as the fully epiphytic hexandrous clade (Penneys & Almeda, 2022). The tribe Pyxidantheae harbours many species that have some form of acarodomatia (Penneys & Judd, 2011). The different types of leaf domatia can be put into eight types as shown in morphological studies on Pyxidantheae done by Penneys & Judd (2011). In addition to hair tuft, (marsupiform) pocket and (recessed) pit domatia, I also show several other domatia types in Figure 1: One type found in this tribe is the lateral laminae domatium (Figure 1, no. 5) in which the entrance of the domatium is protected by small flap-like formations growing from the veins. In pinwheel domatia, which are very similar to lateral laminae, the flaps are bigger and more pronounced as seen in Figure 1, no. 6. Open pocket domatia are named after the protruding tissue growing between main and secondary leaf vein making it an open pocket (Figure 1, no. 3). Belonging to the greater category of pit domatia, coalesced veins domatia (Figure 1, no. 8) have their cavity disguised by the leaf veins. Coalesced veins domatia are also found in another group in the Melastomataceae, the tribe Miconiae (Gutiérrez-Duque & Posada-Herrera, 2025). The only domatia type not growing on the abaxial side of the leaf in the vein axils is the petiolar flap type. It is formed by the petiole of the leaf and has a bulbous shape (Figure 1, no. 7).

In Pyxidantheae, we currently lack knowledge on which mite groups live in the domatia and how the plant-mite relationship really works. The large morphological diversity of acarodomatia in Pyxidantheae is particularly intriguing given that most species occur in a similar habitat, moist rainforests, with supposedly similar requirements for keeping mite mutualists in their domatia. This supposed habitat similarity among Pyxidantheae raises the question of the evolutionary drivers for the formation, loss and diversification of acarodomatia. In Pyxidantheae specifically, it has yet to be confirmed which mites take part in the mutualism and what exact ecological role they play (Penneys & Judd, 2011). Penneys & Judd (2011) proposed that having domatia may be the ancestral state for this tribe and the question how the morphological trait of acarodomatia evolved within this group is still not fully understood. Penneys and Judd (2011 & 2013) performed morphological and genetic studies to unravel the phylogenetic relationships of Pyxidantheae. I am building on their findings regarding the morphological diversity of acarodomatia to explore the evolutionary and ecological aspects of the Pyxidantheae-mite relationship through macroevolutionary analyses and empirical fieldwork.

Since it is not known how acarodomatia evolved within Pyxidantheae, my questions regarding the macroevolutionary history and macroecology were I) how frequent are the different types of domatia across Pyxidantheae, and have different types evolved repeatedly and II) is there a correlation between abiotic conditions, like temperature, precipitation and elevation, and the presence/absence of domatia in the leaves? I hypothesised to find certain rare types to have evolved once in the group while commonly found domatia types like hair tuft, pit and pocket domatia (Myers et al., 2024) may be dispersed throughout the phylogeny. I also hypothesised

that there would be a positive correlation between presence of domatia and precipitation and temperature, due to high productivity in moist and warm habitats and a potentially greater need for protection from herbivores and epiphylls. The microecological questions I posed were III) what arthropods inhabit which types of domatia and does the mite species composition vary, and IV) does microclimate, i.e. sun exposure of the leaf, and age of a leaf play a role in domatia presence? I formulated the last question after noticing differences in domatia presence in different individuals during fieldwork and I hypothesised that microclimate does influence domatia presence. My hypothesis regarding the arthropod inhabitants was that I would find mites in each plant with domatia but that their composition would vary depending on the domatia type. Since it is not known what drives the morphological diversity in this group, I proposed that it may be the different needs of the mite mutualists.

To address my research questions, I examined herbarium specimens of Pyxidantheae, scoring domatia presence or absence and comparing these data with species occurrences paired with climatic data (mean annual temperature, mean annual precipitation, elevation). I performed ancestral character estimations and calculated probabilities of presence and absence and the different types. To explore the evolution of domatia types, I did a qualitative analysis by exploring the distribution of domatia types across the phylogeny. I investigated the microecology by conducting field work in the Cordilleras of the Andes and Sierra Nevada of Santa Marta in Colombia for two months. I sampled eight species of the genus *Blakea* and assessed inhabiting mites and other arthropods and domatia presence and morphology. I initially planned to identify the mites with a DNA-Barcoding approach but was not able to finish this part of the investigation in time to finish my Master thesis. I am planning to identify the samples for a publication on acarodomatia in Pyxidantheae based on this thesis.

Material and Methods

Morphological and macroevolutionary assessment of domatia

To investigate the evolution of acarodomatia in Pyxidantheae, I visually classified domatia in herbarium and online specimens and combined this classification with phylogenetic information. I based my characterisation of domatia types on a publication by Penneys & Judd (2011). I obtained a list of all currently accepted Pyxidantheae species from Penneys et al. (2022) and a trait matrix provided by Darin Penneys (Penneys & Judd, 2011). In this matrix, I had information about the presence of and how distinct domatia are in 74 species. I used GBIF (The Global Biodiversity Information Facility 2024) and Global Plants database by JSTOR as sources for digitized herbarium vouchers, to examine all species that were claimed to have some form of domatia in the data matrix. Additionally, I examined specimens personally at five different herbaria. In Vienna, I was able to examine Pyxidantheae specimens in the herbarium of the University of Vienna (WU). In Colombia, I was provided access to the collections of four different herbaria: Herbario Nacional Colombiano (COL) in Bogotá, Herbario de la Universidad Antioquía (HUA) and Herbario del Jardín Botánico de Medellín "Joaquin Antonio Uribe" (JAUM) in Medellín and Herbario de la Universidad El Valle (CUCV) in Cali. Whenever it was possible for me to see the base of the abaxial side of the leaf, I assigned presence or absence of domatia and types of domatia beyond the 74 species included in Penneys & Judd (2011). With the data matrix and by examining additional herbarium specimens I had the presence and absence and the domatia

types scored for a total of 150 recognised Pyxidantheae species (A1). The list A1 includes names of species I was not able to examine. I included information on domatia absence from Penneys & Judd's (2011) publication for these species.

I wanted to connect molecular and morphological data for the analysis of domatia in Pyxidantheae. To do so, I used the most recent molecular phylogeny of the family Melastomataceae (Penneys et al., 2022). To analyse only the tribe Pyxidantheae, I used the pruned version of the molecular phylogeny, only containing members of this tribe (111 tips), provided by Agnes Dellinger. For all statistical analyses and plots, I used the statistical software R version 4.3.3 (R Core Team, 2023). I plotted the types of domatia onto the phylogeny with the function 'dotTree' from the R package 'phytools' (Revell, 2024). I interpreted the possible evolution of the domatia types in Pyxidantheae visually using clade definitions of Penneys & Almeda (2022). I performed an ancestral character estimation with the domatia types of the phylogeny subset using the equal rates (ER) model and the 'ace' function from the R package 'ape' version 5.0 (Paradis & Schliep, 2019). Additionally, I performed a stochastic character mapping with the domatia types using the 'make.simmap' function from the R package 'phytools' (Revell, 2024) with 100 simulations.

For exploring the macroevolution of mite domatia further, I used the phylogeny of the 111 Pyxidantheae species and the data on domatia presence/absence. I first plotted the presence (1) and absence (0) onto the phylogeny of the 111 Pyxidantheae species with the function 'dotTree' from the R package 'phytools' (Revell, 2024). To explore the evolutionary history of presence of domatia in the tribe, I performed another ancestral character estimation using the same method as before, only with presence/absence data. I performed another stochastic character mapping with 'make.simmap' for the presence/absence data with 100 simulations. I aimed to expand the knowledge on species of Pyxidantheae with domatia to investigate what the probability of presence of domatia in the last common ancestor is. I utilised the same binarized dataset combined with the phylogenetic tree for my macroecological analysis of domatia.

Macroecological analysis of domatia

To investigate whether domatia are more likely to occur under certain environmental conditions, indicating a potential function of phytophagous mites as protection against fungi or algae, I downloaded occurrence data for all Pyxidantheae from GBIF (GBIF Occurrence Download https://doi.org/10.15468/dl.ehjjqa Accessed from R via rgbif (https://github.com/ropensci/rgbif) on 2024-07-04). This initial download yielded 12218 occurrence points across 111 species. I could not include *Blakea muricata* (Lozano) Penneys & Judd in this analysis because there was no georeferenced occurrence data on GBIF. I cleaned this initial dataset of potential false occurrences, such as: occurrences that lay outside of South and Central America, in the ocean, in capital cities, in GBIF headquarters or country centroids, coordinates with identical latitude and longitude, duplicates and coordinates only consisting of zeros. I filtered the occurrence information using the function 'clean_coordinates' from the package 'CoordinateCleaner' (Zizka et al., 2019). After these cleaning steps, I was left with 6443 occurrences for 110 species for subsequent analyses. Next, I downloaded environmental raster layers of bioclimatic variables and elevation at 30 arc sec resolution (ca. 1km at the equator) from WorldClim (Fick & Hijmans, 2017) using the function 'worldclim_global' from the package 'geodata' (Hijmans et al., 2024). For each

occurrence record retained after filtering, I extracted the respective bioclimatic or elevational variables using the function 'extract' from the package 'raster' (Hijmans et al., 2025). For evolutionary analyses, I calculated averages for each climatic variable, as well as elevation, for each species. The final dataset included 110 species, of which all species were also represented in the molecular phylogeny, and averages of all 19 bioclimatic variables WorldClim provides records for. To test whether Pyxidantheae with acarodomatia are more likely to occur in warm and moist environments, I used phylogenetic ANOVAs. I used the 'phyANOVA' function with the equal rates model and 1000 simulations from the packages 'phytools' (Revell, 2024) and 'geiger' (Pennell et al., 2014). I ran three different tests where I used three abiotic variables: the annual mean of precipitation, annual mean temperature and elevation.

Investigation of domatia ecology and inhabitants

To obtain first-hand natural history information on the ecology of mite domatia in Pyxidantheae, I performed two months of fieldwork in Colombia during October and November 2024. During these two months, I travelled with my colleague and specialist in Pyxidantheae Johan Esteban Urrea Cardenas. We visited eight sites throughout the Cordillera Oriental, Cordillera Central and the Sierra Nevada in Colombia with the lowest elevation at 1210 m and the highest at 2600 m (A3). We chose these sites because Pyxidantheae are the most abundant in mountainous rainforests, especially in the Andean mountains of Colombia. We also chose to work in Colombia because we had contacts there who could help us find the individual plants and were familiar with the sites. At each site we spent at least one day scouting for species of the genera *Blakea* and *Chalybea*. We collected material from each species for herbarium vouchers, recorded GPS coordinates for each individual and I screened leaves for domatia. Investigating the leaves meant assessing presence of domatia, searching the leaf lamina for mites roaming it and opening the domatia to extract arthropods living in them. At the first site we found Pyxidantheae, Reserva El Tambo, Nutibara, I opened domatia and collected the arthropods from the plants directly. For the other sites (Table 1), I only assessed domatia presence and searched for mites on the leaves in the field and then collected leaf bases. Within a few days to four weeks after collection, I cut open the domatia under a stereomicroscope and extracted the animals living within with forceps. The arthropods I found in the ethanol of the leaf samples were labelled the same as the animals found on the leaf lamina, since I could not retrace if the arthropods had initially been in the domatia or on the leaf. I identified arthropods, which were not mites, to order or suborder level by using shape and presence of wings, body segmentation, number of legs and shape of the mouth parts. To categorise the arthropods I identified as mites, I used morphotypes, which referred to colour, body shape, leg length or size. Initially, I collected mites to identify them to genus level with DNA-Barcoding (Hebert et al., 2003) but due to a delay in export permits, I was not able to perform this task on the sampled mites and present it in this thesis. I am planning to complete the DNA-Barcoding work following the completion of my Master's degree.

Table 1. All sample sites in Colombia in order of visit.

Site number	Site name	Department	Number of sampled *Blakea* species	*Blakea* species found (underlined if sampled, * with domatia)
1	Valle de Mariposas	Boyacá	0	*B. parasitica*, *B. watsonii*
2	Reserva El Tambo	Antioquía	2	*B. andreana*, *B. sp. nov. 2*, *B. sp. nov. 3*, *B. sp. nov. 4*, *B. sp. nov. 5**, *B. sp. nov. 6*
3	Reserva El Globo	Antioquía	2	*B. argentea*, *B. quadrangularis**
4	La Mina	Antioquía	1	*B. quadrangularis**
5	Reserva Cerro El Ingles	Valle del Cauca	2	*B. henripittieri**, *B. sp. nov. 7**
6	El Queremal	Valle del Cauca	1	*B. sp. nov. 8**, *B. sp. nov. 9*
7	Doña Dora	Valle del Cauca	2	*B. henripittieri**, *B. podagrica**
8	Reserva ProAves El Dorado	Magdalena	0	*B. granatensis*

To assure even sampling in my assessments of leaf mites, I sampled at least five leaves of three age stages per species and, when possible, per individual plant. I decided to sample different age stages because I wanted to assess whether all domatia are inhabited regardless of leaf age. Older leaves may have been grown under slightly different abiotic conditions and therefore may have different mite abundance and or composition. I classified the first fully developed leaves (usually fresh green, without epiphytes) on a branch as "young"; leaves on a node below those I classified as "medium" and I classified any leaves below the node of medium leaves as "old" (leaves with variable degrees of epiphytic growth and traces of herbivory). I recorded the presence of domatia for each leaf. In total, I sampled leaves of five species from up to five different individuals per species to collect inhabitants of domatia. Besides these species, I gathered leaf roaming mites from *Blakea andreana* Cogn. and *Blakea argentea* Gleason, which both did not have domatia. I provide an overview of individual counts and sample sizes in Table 2.

Table 2. List of all sampled *Blakea* species and the respective sample size regarding leaves in which I searched for animals. Domatia presence is indicated by 1, absence as 0.

Species	Domatia presence	Individuals	Leaves sampled total
B. andreana	0	1	15
B. argentea	0	1	19
B. henripittieri	1	3	77
B. quadrangularis	1	5	129
B. podagrica	1	1	24
B. sp. nov. 5	1	3	35
B. sp. nov. 7	1	1	31
B. sp. nov. 8	1	2	59

To explore whether different species of Pyxidantheae differ in the number of arthropods on the leaves and in the domatia, I plotted the total and relative abundance of arthropod groups for each species using stacked barplots. I calculated relative abundance by dividing the number of animals found by the number of sampled leaves. The result can be seen as average number of animals found per leaf. To quantify differences in arthropod diversity among species, I calculated the Shannon diversity index utilising my morphotypes in mites and arthropod group categorisations per *Blakea* species using the function 'diversity' from R package 'vegan' (Dixon, 2003). Additionally, I performed a Chi-Squared test to see if different groups of arthropods differ in abundance depending on leaf age. I also ran a Chi-Squared test for the combined effect of species and age on arthropod abundances.

Microclimatic investigation on *Blakea quadrangularis*

One species, *Blakea quadrangularis* Triana, varied in the presence and absence of domatia, with domatia present in only some leaves. This gave me the opportunity to investigate whether microclimatic factors such as sun exposure may affect domatia development. In *B. quadrangularis,* I assessed at least 100 leaves per individual, across five individuals, and 1081 leaves in total (Table 3). I also noted sun exposure of the branches sampled, which I categorised qualitatively with three levels of exposure (3 = sunny and exposed, 2 = shade and some chance of direct sunlight, 1 = no direct sunlight and very shady). I recorded this because I hypothesised that leaves in moist, shady habitats with high productivity may need more protection by mites from epiphytes than the ones that grow in a sunny environment. I expected to find domatia rather in shaded than exposed leaves. To test if presence and absence of domatia is dependent on microclimate and leaf age in *B. quadrangularis,* I performed two separate Chi-Squared tests.

Table 3. List of all *Blakea quadrangularis* samples for domatia presence absence assessment. Sun exposure is encoded as 1= no direct sunlight and very shady, 2= shade and some chance of direct sunlight, 3=sunny and exposed. Young, Medium and Old are the leaf age categories I used.

Individual	Sun exposure	Young	Medium	Old	Total sampled leaves
1	2	75	53	55	183
2	3	64	42	69	175
3	1	38	33	65	136
4	1	72	46	95	213
5	2	42	31	77	150
5	1	84	56	84	224

Results

Morphological and macroevolutionary assessment of domatia

In Penneys & Judd (2011), a total of 30 of the currently accepted 208 Pyxidantheae species (Penneys et al., 2022) were scored as having domatia. From this complete Pyxidantheae species list, I was able to re-evaluate 150 species across approximately 260 herbarium specimens (~200 in Colombia, ~60 from Vienna and online herbaria). I found domatia to be present in 56 of these 150 species, so ca. 33% of the complete Pyxidantheae species list (A1) were identified as having domatia here. This increases the estimate of Penneys and Judd (2011) by 26 species. Of the 111 species included in the Pyxidantheae phylogeny, 44 species had domatia and 67 did not have domatia. If I extrapolated the 33% to the whole species list, I would expect that 69 of the currently described 208 Pyxidantheae species may have domatia.

In my Pyxidantheae dataset on domatia presence and types (A1), I had recorded some types more often than others and could not score one definitive type for some species. Marsupiform pockets were the most common domatia type, occurring in 12 species, 21.4% of the 56 species with domatia. The next largest group consisted of 11 species with pinwheel domatia (19.6%), including all *Chalybea* species except *Chalybea penduliflora* (Wurdack) M.E.Morales & Penneys. I recorded coalesced veins domatia in nine species (16.1%). Hair tuft domatia were present in eight species (14.3%), and another eight species exhibited either multiple domatia types or intermediate forms (14.3%). Recessed pit domatia occur in five species (8.9%), petiolar flap domatia in two (3.6%), and lateral laminae domatia in one (1.8%). No species exclusively possessed open pocket domatia. *Blakea dodsoniorum* (Wurdack) Penneys & Almeda is the only species in which I observed open pockets, though in some herbarium specimens, no domatia were present or the structures resembled lateral laminae more closely.

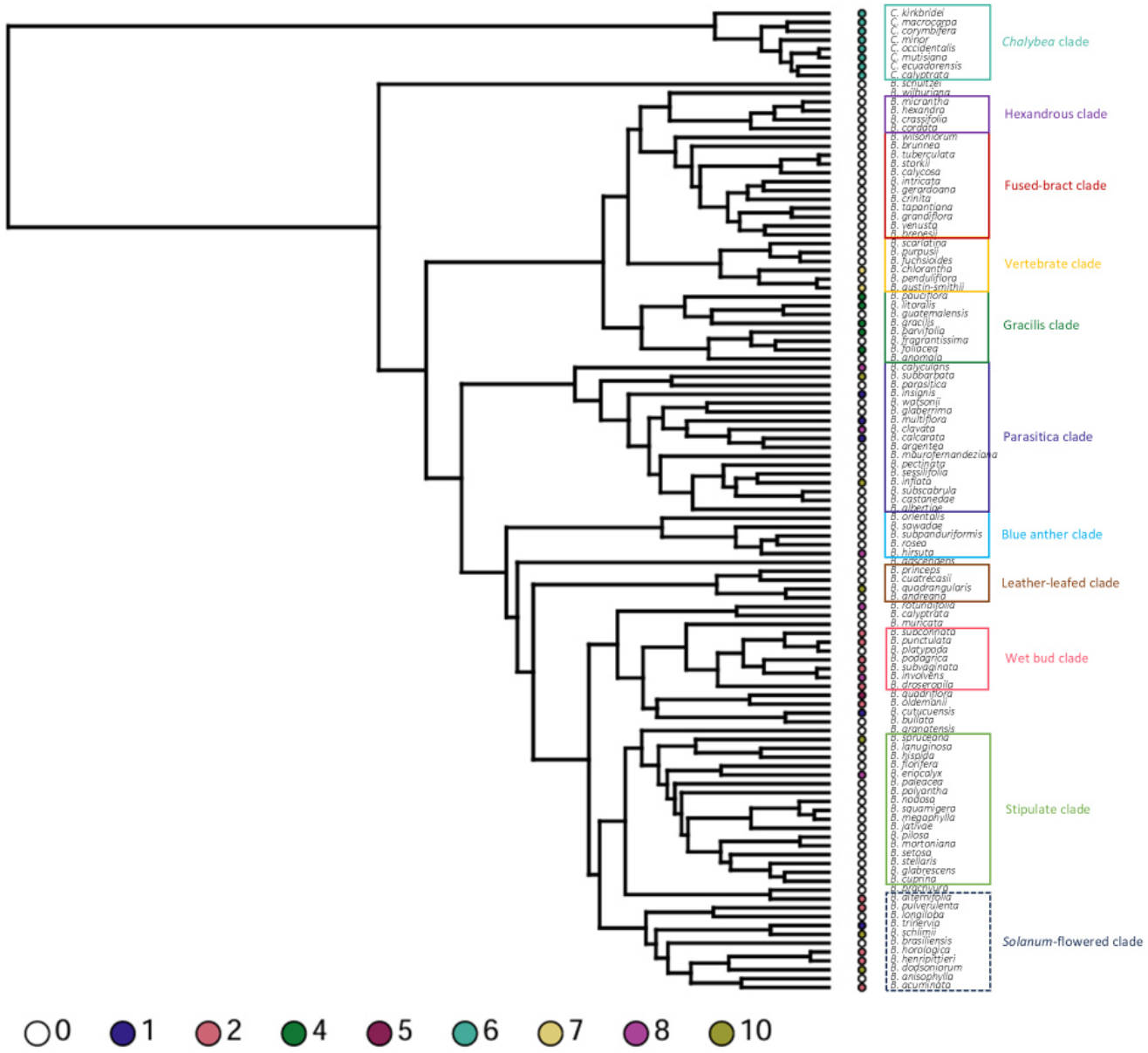

Figure 2. Mapping of types of domatia on Pyxidantheae phylogeny: 0=domatia absent, 1=hair tufts, 2=marsupiform pocket, 4=recessed pits, 5=lateral laminae, 6=pinwheel domatia, 7=petiolar flap, 8=coalesced veins, 10=multiple types of domatia or hybrid form. Number 3 would have been open pocket domatia but there are no representative species in the phylogeny, number 9 are revolute margin domatia which don't occur in Pyxidantheae but Merianiae. Clades are marked after (Penneys & Almeda, 2022). The *Solanum*-flowered clade mark here, falsely includes species that have not been placed yet: *Blakea brasiliensis* Cogn., *Blakea pulverulenta* Vahl, *Blakea schlimii* (Naudin) Triana, *Blakea trinervia* L.; *Blakea parvifolia* and *B. subbarbata* are unplaced too according to Penneys & Almeda (2022) but are marked here as being part of the Gracilis and Parasitica clade respectively.

Mapping the eight different domatia types on the Pyxidantheae phylogeny, I could see some trends of where on the phylogeny the types are located, i.e. which types have evolved multiple times and which are restricted to a certain clade (Figure 2). One domatia type, open pockets, is not represented in the phylogeny since there is no species that exhibits this type exclusively. Pinwheel domatia (Figure 1, no. 6) are exclusively found in *Chalybea,* which is sister to the genus

Blakea. They occur in all *Chalybea* specimens I was able to assess, apart from the aforementioned *C. penduliflora*. It is very likely that the root state of *Chalybea* had domatia of the pinwheel type, while the root state of *Blakea* likely lacked domatia. The evolution of domatia in *Blakea* probably happened relatively recently, given that the majority of deeper nodes are reconstructed with a 100% probability of lacking domatia. I found hair tuft domatia scattered throughout the whole tribe (Figure 3). The same can be said for marsupiform pockets, lateral laminae and coalesced veins suggesting multiple evolutionary origins for these types in Pyxidantheae. Absence of domatia occurs throughout the tribe but is noticeably more common in certain clades. The hexandrous and fused-bract clades, for example, do not contain any species with domatia. In the stipulate clade there are only three species with domatia (*Blakea spruceana* Cogn., *Blakea eriocalyx* Wurdack, *Blakea alternifolia* Gleason) and they all exhibit different types of domatia. The vertebrate-pollinated clade is the only one with species growing petiolar flap domatia, which are *Blakea chlorantha* Almeda and *Blakea austin-smithii* Standl. In the Gracilis clade, most species have recessed pit domatia, apart from three species (*Blakea guatemalensis* Donn.Sm., *Blakea fragantissima* (Almeda) Penneys & Almeda, *Blakea anomala* Donn.Sm.). In addition to the qualitative assessment of Figure 3, I performed an ancestral character estimation with the different domatia types. I found there are 41.33 changes on average per tree between domatia types across the 100 simulations. The transition rate from one type to another according to my calculations is 0.02 per unit time (million years). I present the root probabilities from the ancestral character estimation and the pairwise change rates calculated with stochastic character mapping in A2.

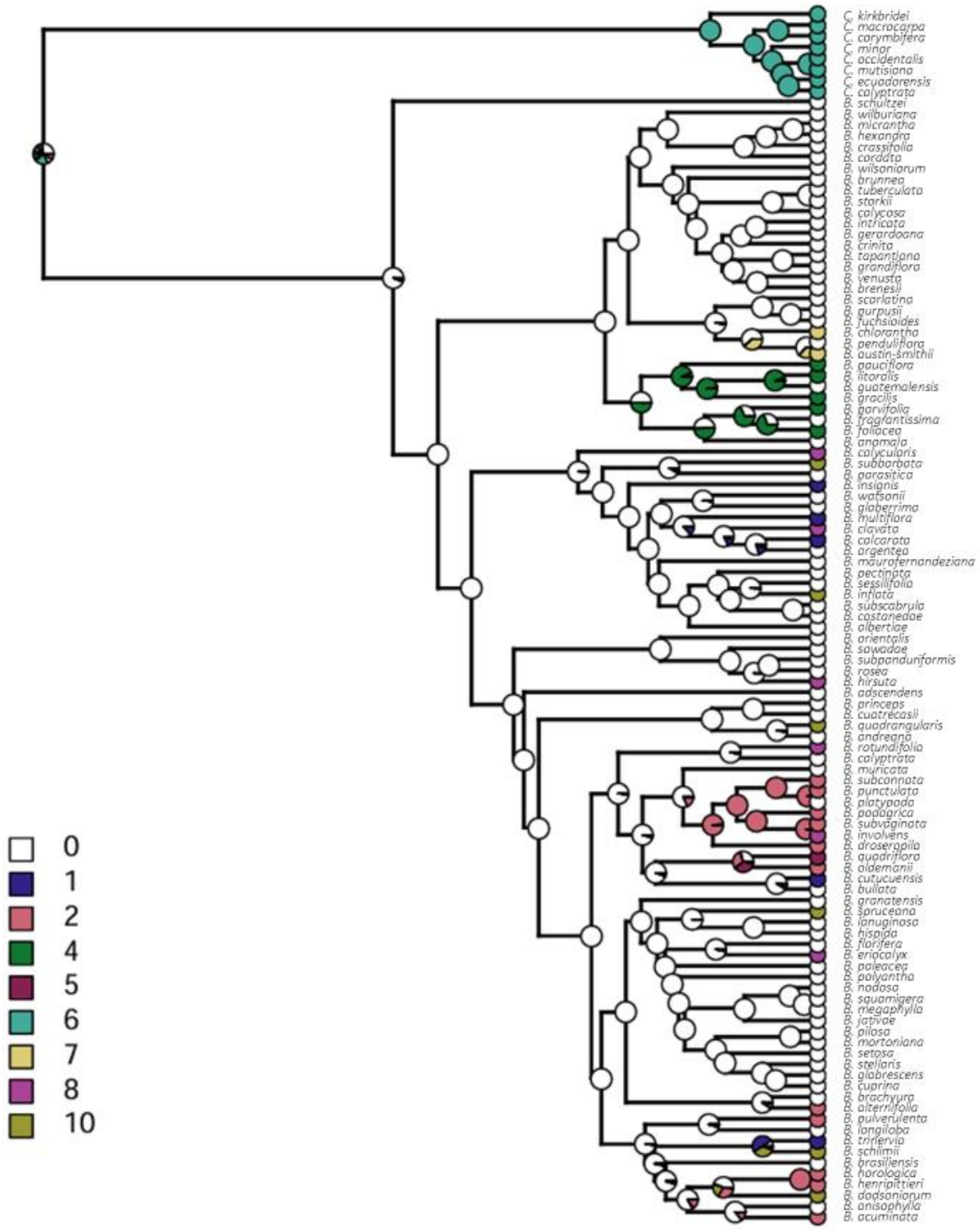

Figure 3. Reconstruction of the evolutionary history of domatia types; the root of Pyxidantheae is reconstructed as equivodal, with 11% probability of having no domatia or any of the types of domatia. 0=domatia absent, 1=hair tufts, 2=marsupiform pocket, 4=recessed pits, 5=lateral laminae, 6=pinwheel domatia, 7=petiolar flap, 8=coalesced veins, 10=multiple types of domatia or hybrid form. Number 3 would have been open pocket domatia but there are no representative species in the phylogeny, number 9 are revolute margin domatia which don't occur in Pyxidantheae but Merianiae. Figure made with 'make.simmap' function using the ER model; nsim = 100.

In order to broadly understand the evolutionary background and ensure sufficient replication for analysing links to climatic variables I reconstructed the evolutionary history of domatia presence/absence. I found that the probability of the root of Pyxidantheae to display presence of domatia is 49.3%, for absence of domatia it is 50.7%. On average across the 100 simulations, there are 28.47 state changes from domatia absence to presence, and 25.04 changes vice versa. This amounts to 53.51 state changes per tree in total. The transition rate from one state to the other according to my calculations is 0.18 per unit time (million years). The probability for a species tip to display absence of domatia is 61.3% and for presence 38.7%. I provide a graphical depiction of the trait probabilities in Figure 4. In summary, it is very unclear if the root state for Pyxidantheae had domatia and if yes, what type of domatia would have been present.

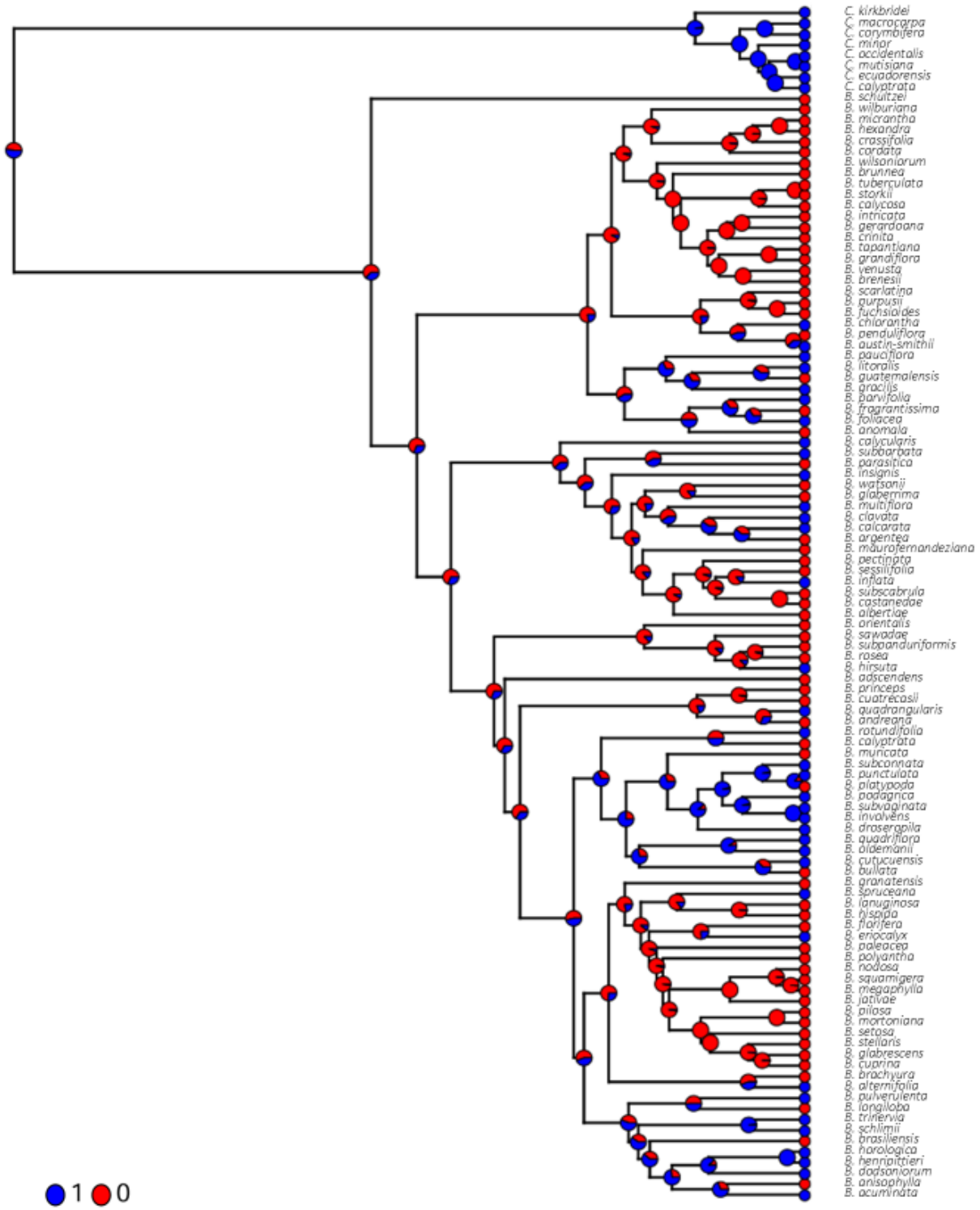

Figure 4. Reconstruction of the evolutionary history of domatia presence (blue) or absence (red); the root of Pyxidantheae is reconstructed as equivodal, with 49% probability of having domatia; domatia have been gained and lost repeatedly in the evolutionary history of Pyxidantheae. Figure made with 'make.simmap' function using the ER model; nsim = 100.

Macroecological analysis of domatia

The phylogenetic ANOVAs were not significant, neither for mean annual temperate (p-value=0.453) nor for mean annual precipitation (p-value=0.691), nor for mean elevation (p-value=0.48). This suggests that species with domatia do not grow in different macroclimates than species without domatia. Overall, I found Pyxidantheae to grow in elevations from 34 to 2539 meters, in mean annual temperatures from 12.4°C to 26.4°C with an average precipitation of 805 to 6857 mm (Figure 5).

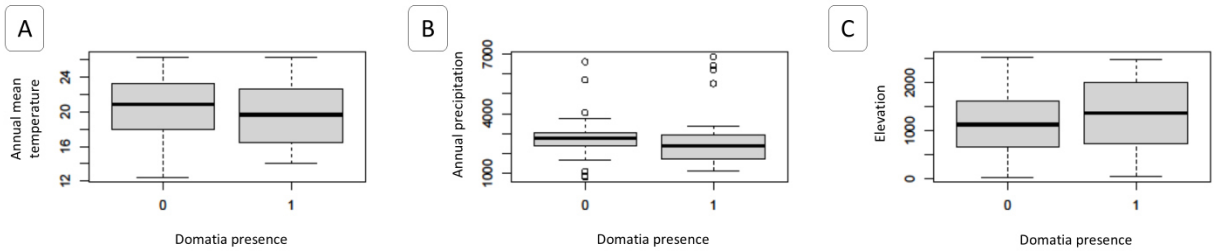

Figure 5. Boxplots with distribution of averages of the abiotic factors of Pyxidantheae included in phylogeny and Pyxidantheae species divided by domatia presence (1) and absence (0). A: Annual mean temperature; B: Annual precipitation; C: Mean elevation.

Domatia ecology and inhabitants

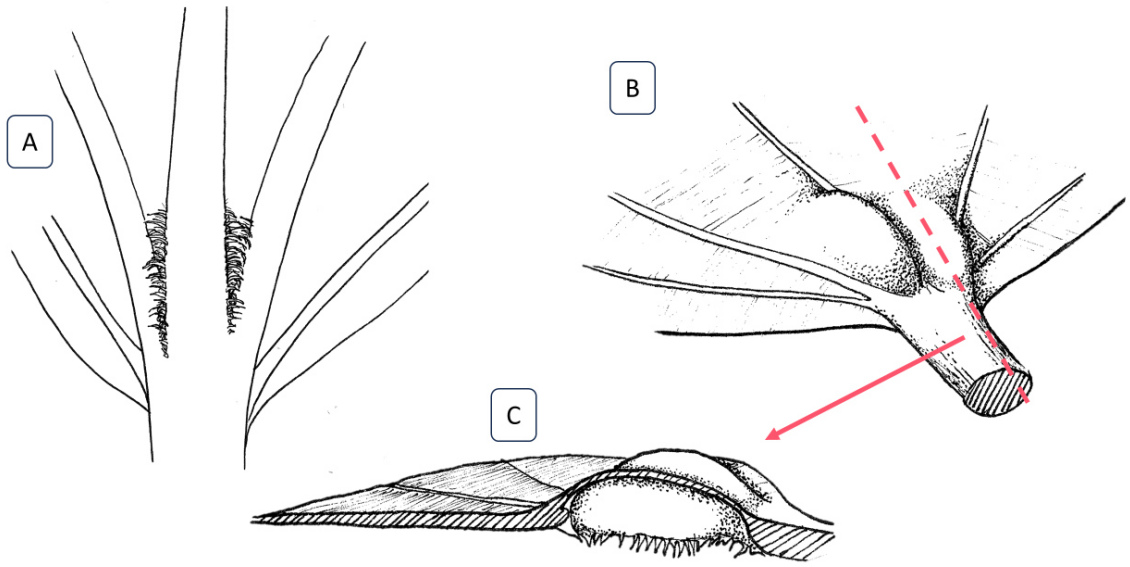

Figure 6. Schematic depiction of domatia of *B. sp. nov. 5*; A: Leaf underside, thick hairs protect the entrance to the domatia; B: Leaf upside, small protrusions between primary and secondary veins; C: Longitudinal cut through domatia showing the cavity that gets protected by hairs.

Across eight field sites, I was able to sample eight different *Blakea* species, six of which had domatia. I sampled two *Blakea* plants without domatia because I encountered mites roaming the leaves. The domatia types of the five species with domatia were either combinations of hair tuft domatia and marsupiform pockets or marsupiform pockets and coalesced veins. *Blakea sp. nov. 5* was different compared to the domatia in other Pyxidantheae. This new *Blakea* species exhibited

cavities that protruded on the abaxial side of the leaf as small humps with the opening disguised by large trichomes (estimated 1-3mm long). The trichomes in this particular species were far larger than in other hair tuft domatia and did not grow directly between two diverging veins but their growth concentrated on the first 1-2cm of the primary leaf vein (Figure 6). In *B. quadrangularis* the domatia seemed like hair tuft domatia on first glance but had a small pocket between primary and secondary veins, similar to coalesced veins. Other individuals had distinct tissue between these veins, like the marsupiform pockets. Hair density varied as seen in Figure 7.

Figure 7. *B. quadrangularis* variation in domatia: left photo shows domatia with a lot of hairs protecting the cavities, middle photo shows sparse hairs on the domatia; right photo shows tissue growing between primary and secondary veins and a few hairs protruding from the domatia.

Across all sampled *Blakea* species, I encountered mites and other arthropods in varying numbers (Figure 8) apart from *Blakea podagrica* Triana. In this species, I only found eggs, for this reason I did not include it in Figure 8. Finding mites in every species besides *B. podagrica* was in line with my expectation of finding mites in every Pyxidantheae plant with domatia. I found the highest number of mites relative to sampling effort in *Blakea sp. nov. 8*, 38 in total. Using morphotypes as identifiers, I saw many of the same mites in the same *Blakea* species. However, I found a variety of different morphotypes, in both *B. henripittieri* and *B. sp. nov. 8*. Besides mites, the number of other small arthropods (all of them insects apart from one spider was high. When I compared abundances of animals in the different Pyxidantheae species, I found that *B. sp. nov. 5* had the highest count, relative and absolute. In *B. sp. nov. 5,* I encountered 75 Hemiptera belonging to the family Coccidae and 17 other, unidentified Hemiptera, making this order the most dominant group by far in this species. *B. quadrangularis* had the lowest animal count relative to sampling effort. I found a large number of unidentifiable eggs in this species which are not accounted for in Figure 8 or further analysis. I found that the composition and abundances of the different arthropods are independent from leaf age (p-value = 0.4419) and the same is true for the combined factor of plant species and leaf age (p-value = 0.2793). I provide a bar graph depicting arthropod abundances per leaf age and species in A4.

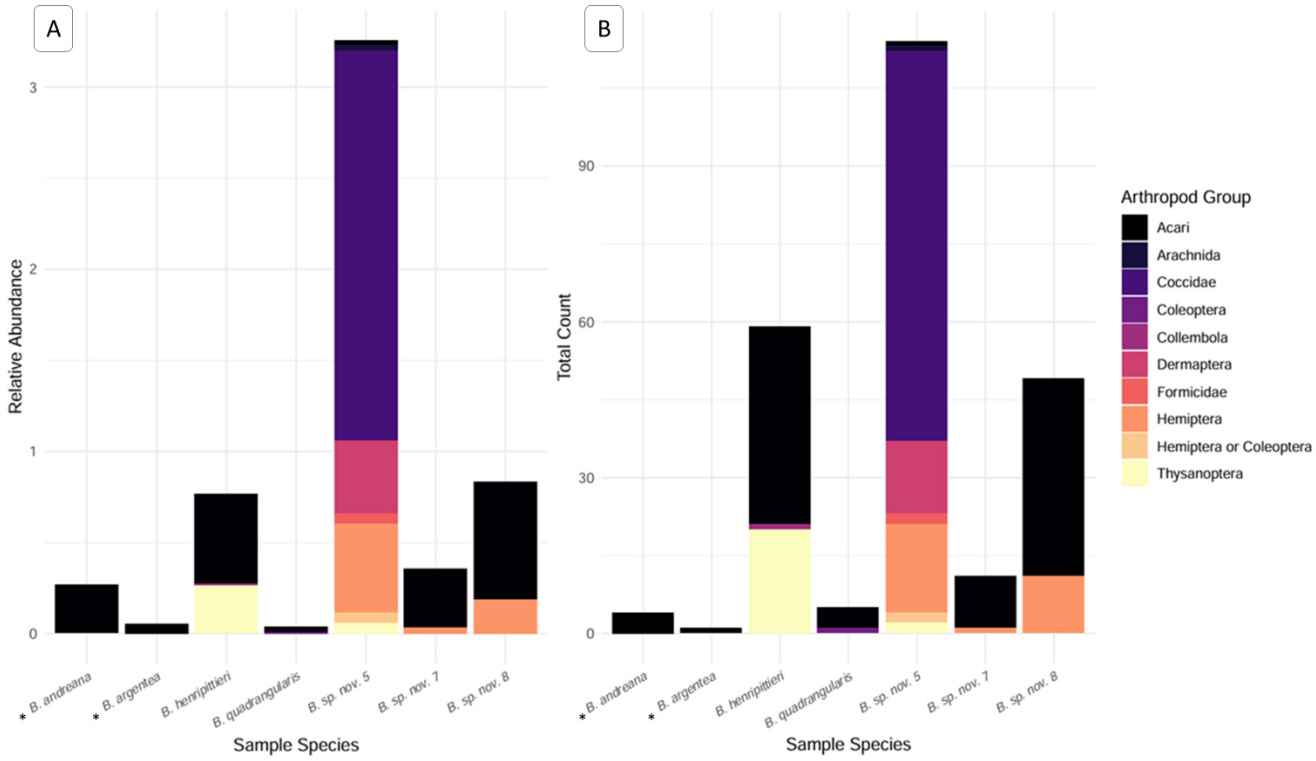

Figure 8. A: Abundance of arthropods per sample species relative to sample effort. B: Absolute abundances of arthropods in the different sample species. * indicates species without domatia. Eggs are excluded in this graph.

According to the results of the Shannon diversity index, the diversity of animals found in the acarodomatia and on the corresponding leaf is highest in *B. sp. nov. 5* and lowest in *B. andreana* and *B. argentea* (Table 4). I only found 3 of the same mites on a leaf in *B. andreana* and 1 mite on *B. argentea*, both species without domatia. Due to that, their Shannon index was zero and I did not include *B. andreana* and *B. argentea* in Table 4. The other *Blakea* species have very similar indices.

Table 4. Shannon index values for the different *Blakea* species.

Species	Shannon index
B. henripittieri	0.6565277
B. quadrangularis	0.6365142
B. sp. nov. 5	1.9701814
B. sp. nov. 7	0.6365142
B. sp. nov. 8	0.6057975

Microclimatic investigation on *Blakea quadrangularis*

In contrast to macroclimate, microclimatic conditions seemed to have a strong effect on domatia formation in *Blakea quadrangularis*. My hypothesis was that there is a connection between the immediate environment of a leaf, i.e. microclimate and the presence of domatia. I could confirm my hypothesis, by testing if the presence of domatia in a leaf is dependent on sun exposure (p-value<0.01). Leaves from sun-exposed individuals had significantly fewer domatia than leaves growing in the shade. The age of a leaf also played a role in domatia presence (p-value<2.2e-16). Across individuals, older leaves had significantly fewer domatia than younger leaves (Figure 9).

Overall, individuals varied largely in the presence of domatia, with individuals ranging between 23.4% to 95.2% domatia in young leaves and 7.2% to 98.8% domatia in old leaves.

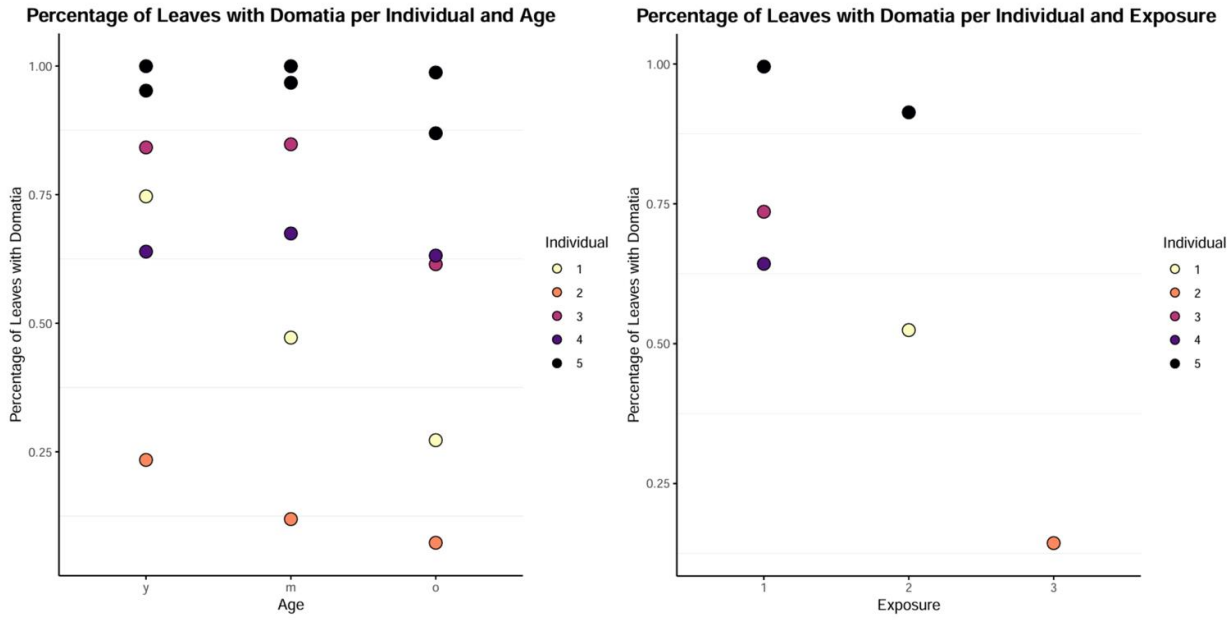

Figure 9. Percentages of leaves with domatia per individual and age (left) and per exposure (right) in *B. quadrangularis*.

Discussion

Summary of results

In this study, I expanded the knowledge on acarodomatia in Pyxidantheae, identifying 56 species with domatia out of the 150 I examined. I performed an ancestral character estimation with presence and absence of domatia and found that the probabilities for both states were approximately 50% and therefore inconclusive. By examining herbarium specimens and live individuals, I concluded that the trait might be more plastic than previously thought. Some members of Pyxidantheae exhibited different domatia types, intermediates or lacked domatia only in some leaves. Marsupiform pockets were the most common type in my investigation and probably evolved multiple times within the tribe. Hair tuft, lateral laminae and coalesced veins domatia all might have had multiple evolutionary origins too. In my macroevolutionary analysis, I found no significant correlation with domatia presence and absence and climatic factors (temperature, precipitation, elevation). I found evidence in *B. quadrangularis* that microclimate, more than macroclimate, influences the development and subsequently presence of domatia in different leaves. Sun exposure seems to be a big factor but there was also a trend in older leaves being less likely to have domatia than young leaves. The arthropods I found in the sampled species always included mites, but arthropod composition varied between plant species. *Blakea sp. nov. 5*, a species yet to be described, showed the biggest diversity out of all sampled *Blakeas*.

Morphological and macroevolutionary assessment of domatia

By assessing herbarium specimens, I have added more species with presence of acarodomatia than previously recorded, making the total of Pyxidantheae with acarodomatia 56 species, thereby almost doubling the number of species with domatia. With these additional species, the ancestral character state reconstruction was inconclusive as opposed to Penneys & Judd's (2011) findings that the last common ancestor probably had domatia. This is probably also due to their study being published almost 15 years ago and the difference in the methods of our studies. The level of knowledge regarding Pyxidantheae has greatly advanced since then, as shown by many newly described species and different taxonomic classification inside of Pyxidantheae (Penneys & Almeda, 2022). It is highly likely that domatia presence evolved multiple times even within the tribe Pyxidantheae as I show in Figure 3 and 4. There are multiple gains and losses which point to the evolutionary lability of the trait. The drivers of these changes have yet to be discovered. It could be differences in climatic conditions and microclimate, which I will expand on going forward.

Contrary to my hypothesis regarding a connection between moist and warm habitats, I did not find any correlation with overarching climatic conditions. Additionally, my findings are indirectly opposing Myers et al.'s (2024) findings that there are less plants growing acarodomatia at lower latitude, since Pyxidantheae grow in the Neotropics and at least 56 species of the 208 described species have domatia. But since their study was a global assessment and they illustrated general trends, this may not apply to Pyxidantheae.

In line with Myers et al. (2024), I found multiple evolutionary origins of domatia and of the different types of domatia. I was able to confirm my hypothesis that different, common domatia types are scattered throughout the phylogeny of Pyxidantheae, like hair tufts, marsupiform pockets and coalesced veins; but that other, rarer types are restricted to certain clades. Recessed pits and petiolar flap domatia probably each only evolved one time in the Pyxidantheae because they only occurred in their respective clades (Gracilis clade and vertebrate-pollinated clade respectively). Pit and petiolar domatia occur in multiple species across angiosperms but to investigate why they evolved, we first have to find out if they differ in function compared to other types and what the needs of the prospective tenants are. Another finding of Myers et al. (2024) was the presence of pit domatia in wetter climates, and more species with hair tuft domatia in drier, more temperate ecosystems. Following the definition of pit domatia employed by Myers et al. (2024), this would include coalesced vein domatia and recessed pit domatia in Pyxidantheae. I found pit domatia 14 times, which is more often than hair tuft domatia, which I found 8 times. This would be in line with their findings that pit domatia are more common than hair tufts in the tropics. One theory is that trichomes can be a breeding ground for potentially harmful fungi or bacteria in wet and warm climates and may hence be selected against (Kim, 2019).

I have also found many intermediates in domatia categories when reviewing herbarium specimens and live plants, especially often involving in-between forms of marsupiform pockets and coalesced veins. This makes me pose the question: are these types functionally different or was it chance and geographic isolation that different types evolved? I hypothesize that these intermediates may show an evolutionary trend towards one uniform domatium in certain clades of Pyxidantheae. I suggest to future investigators to define and analyse genes that affect the

development of domatia, similar to an approach taken by Chomicki et al. (2024). In their study, they defined genes that are involved in trichome development and as candidate genes for domatia development. Chomicki et al. (2024) proposed *Vitis vinifera* L. as a model system to explore other genes involved in tuft domatia development. In future investigations, knock-outs of these candidate genes could be produced and their leaves anatomically compared to the wildtype's leaves. Nishida et al. (2005) found that cell differentiation in the mesophyll is most likely responsible for the pocket formation in *Cinnamomum camphora* (L.) J.Presl. This means to investigate the development of pit and pocket domatia, one could analyse the influence of cell differentiation genes.

In future studies, one should also compare the ages of lineages in which intermediates are found to answer whether this is a recent evolutionary trend or even a tendency at all. It could also be possible for these intermediates to be evidence of the plasticity in this trait. I found that not every leaf in domatia-bearing species develops domatia, which is another testament to plasticity. Future research should try to determine if environmental conditions like shade, competition with other plants or mite availability may play a role in the development of acarodomatia.

Ecology of acarodomatia in Pyxidantheae

In my results I provide evidence that my hypothesis on microclimate influencing domatia presence is right. In my investigations on *B. quadrangularis,* I found evidence in a species with domatia that sun exposure correlates with absence or presence of domatia. During fieldwork I observed one individual growing very exposed on a palm tree with almost no shade, while another individual grew a few meters next to it, close to the ground and shaded by surrounding shrubs. The exposed *B. quadrangularis* plant did not have domatia in most leaves, while the other individual had domatia present in almost all leaves. This could of course be attributed to individual effects, since this observation can also be due to genetic differences of these individuals, although they are likely close relatives given their proximity. In the macroevolutionary analysis I also found that the hexandrous clade of Pyxidantheae has no records of species with acarodomatia. This is probably due to this clade being a group of epiphytes that presumably receive a lot of sun exposure (D. Penneys, personal correspondence). High sun exposure may reduce stress by epiphylls, since leaf surfaces can have extremely high fluctuations in temperatures and moisture levels (Hirano & Upper, 2000; Lee et al., 2023). This would make it hard for fungi, algae and bacteria to grow but also for mites to live as mutualists on the Pyxidantheae plant. My investigations lead me to hypothesise that immediate environmental conditions constitute domatia presence or absence more so than macroclimatic conditions in Pyxidantheae. In future studies, there should be efforts made to test individual effect versus microclimate (sun exposure and humidity) in regard to domatia presence. For a more quantitative approach, one could record sun exposure and surrounding humidity of each leaf of different individuals in the same domatia-bearing species with a MultispeQ device and record the domatia presence. The MultispeQ is a device that is usually used for measuring photosynthetic activity but records light intensity and humidity too (Kuhlgert et al., 2016). With this approach one could explore, if various branches of the same plant display different domatia presence or absence ratios due to different microclimate. To confirm my hypothesis, that microclimate constitutes domatia presence more research is required, the approaches of which I have outlined earlier.

Another observation of mine was that the presence of domatia can also vary with leaf age, possibly due to seasonality. Although Pyxidantheae grow in the wet tropics near the equator where temperatures tend to be similar throughout the year, there are dry and rainy seasons (Urrea et al., 2019). In Urrea et al.'s (2019) study, they found that the Cordilleras in Colombia experience seasons in a bimodal scheme with two dry and two rainy seasons per year. This could mean different needs for mites and plants depending on varying levels of moisture and, as a consequence, different growth of epiphylls. This would result in seasonally dependent development of domatia and change in the mutualism throughout the year. In accordance with this hypothesis of seasonality-dependence, Richards & Coley (2012) discovered that domatia entrances varied depending on the season they surveyed *Psychotria horizontalis* Sw. plants in. They found that the domatia openings were smaller relative to domatia size in the dry season compared to the wet season. Richards & Coley (2012) also found different mites in the dry season and the wet season. They showed the influence seasonality has on both domatia and the mite composition. In my own study, I found a lot of unidentifiable eggs, instead of adult arthropods, in *B. podagrica,* which may be another indication that seasonality influences domatia ecology, leading to a seasonal turnover in domatia inhabitants. The eggs I found might belong to mites, but they could also belong to another small arthropod. As stated before, researchers investigating the ecology of domatia should sample plants with acarodomatia in different seasons.

Similarly, in a study by Parolin et al. (2011), old leaves exhibited domatia more frequently and harboured more predatory mites than younger leaves. In contrast, I found older leaves of *B. quadrangularis* to exhibit domatia less frequently than younger leaves. Since Parolin et al. (2011) worked on *Viburnum tinus* L., a plant in a different family and growing in dry temperate regions (Parolin et al., 2011), these results are not immediately comparable to mine. Overall, I believe that the seasonality effect is stronger than an age effect (i.e., loss of domatia with age) in Pyxidantheae (also see Figure 9). I hence hypothesise that older leaves of *B. quadrangularis* had fewer domatia due to those leaves being formed in a different season, where mite mutualisms were less beneficial than in the season in which I sampled them. Further research investigating effects of seasonal differences on domatia-bearing plants in the tropics is needed. I suggest exploring the leaf longevity, timepoints of leaf formation i.e. when in the year, presence of domatia and the length of seasons at the sites Pyxidantheae grow at. This could shed light on climatic influences on domatia formation, if paired with assessment of presence or absence of domatia throughout seasons.

Inhabitants of the domatia

I was able to compare eight species of *Blakea* in regards to arthropod abundance in their leaf domatia. I found that the abundance of different arthropods and leaf age are independent from each other. Given small sample sizes and low abundances (below 5 mites per sample), the result of the Chi-Squared test may not be reliable. Mites would have needed to make up more than 20% of my data points for results to be fully conclusive (DATAtab Team, 2025). For a more accurate analysis, I will use either pooling of the low abundances or another test for independence in the future. Not only abundance but also composition was part of my research questions. With the Shannon diversity index, I was able to account for uneven abundances in assessing arthropod diversity. Out of all sampled species, *Blakea sp. nov. 5* was the species with the highest diversity. This species grows in the remote natural reserve El Tambo, in the county Antioquia of Colombia.

The broader region comprises the edge of the western Cordillera and borders the Chocó area, which is mostly plains under climatic influence of the Pacific Ocean (J. Urrea Cardenas, personal correspondence). *Blakea sp. nov. 5* therefore grows in an ecotone region. Ecotones are characterised by rich diversity due to two ecosystems meeting (Kark, 2013), which may have contributed to the comparably high diversity in *Blakea sp. nov. 5*. Another reason could be that the reserve is, with the exception of a few pastures for grazing cattle, largely untouched by human influence. Little disturbance by humans could mean higher diversity in this area (MacDougall et al., 2013). The inhabitants of domatia are only a small, but maybe more vital than we think, part of the vast diversity plants facilitate.

At the start of my thesis, I posed the question, what arthropods inhabit which types of domatia and whether the mite species composition varies? Although I was not able to identify the mites I found yet, I saw a variety of morphotypes, especially in *B. henripittieri* and *B. sp. nov. 8*, which both exhibited some form of pocket domatia. I suspect many of the longer legged mites to be predatory while many of the smaller mites may be eating microorganisms like bacteria, fungi and algae (*Identifying Mites*, 2021, accessed on 2025-05-15 https://www.youtube.com/watch?v=NN82bM2sN0s). As stated before, I am planning to further identify these mites to adequately put them into categories regarding their feeding habits to further explore their potential role as mutualists or pathogens. It remains to be seen whether the mites I found belong to groups already found by Pemberton & Turner (1989). In their study on a variety of plants across ecosystems, they found Phytoseiidae, Stigmataeidae and Ascidae known to belong to predatory mites and fungivorous mites of the families Tarsonemidae and Winterschmidtiidae and the order Oribatida, which I would expect as well. It will be particularly interesting to know if the Pyxidantheae I sampled harboured phytophagous mites from Eriophyidae, since these are known to inhabit leaf domatia too (Nishida et al., 2005; Pemberton & Turner, 1989). Nishida et al. (2005) and Richards & Coley (2012) found that opening size and the space available inside a domatium constitute which mites can be found. Further studies investigating mite populations relating to domatia type and size are needed, especially for tropical mutualisms.

Conclusions

My thesis represents a broad preliminary exploration of the evolution and ecology of acarodomatia in Pyxidantheae. I provide a valuable addition to tropical mite-plant mutualisms with my work, because I investigated multiple aspects of the interaction in my study system. I added records of species with domatia, almost doubling the known records to 56 Pyxidantheae species bearing domatia. Additionally, I found evidence of multiple evolutionary origins of leaf domatia in this group. I showed that marsupiform pockets is the most common type in Pyxidantheae and that it likely evolved more than once. With my macroclimatic analyses, I could show that there is no correlation with the presence or absence of domatia and mean annual temperature, precipitation and elevation. However, I laid the basis for further research into the influence of microclimatic conditions on domatia presence and mite inhabitants through my empirical fieldwork, emphasising the dire need of such natural history field studies. I have also gathered samples of arthropods to identify in the future both morphologically and by using DNA-barcoding, which will add knowledge about possible mutualistic partners in mite-plant

relationships. One of the most novel discoveries of my thesis is the possible effect of seasonality on the development of acarodomatia and the interaction as a whole. I propose future research should focus on each of these topics in tropical acarodomatia: the morphology, macroecology, microecology. To investigate the morphology, studies should include which genes might be responsible for the development of domatia and try to quantify the categories we now use in Pyxidantheae by measuring entrance and volume of the cavities. To investigate the macroecology in acarodomatia in Pyxidantheae, especially regarding the diversity in domatia types, one should explore the potential effect of seasonality on domatia. And lastly, to study the microecology, future investigations should test the effect of microclimate i.e. sun exposure and humidity on domatia development.

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Appendix

A 1. All Pyxidantheae species; Domatia presence: 0=no domatia, 1=domatia; Domatia types: 1=hair tufts, 2=marsupiform pockets, 3=open pockets, 4=recessed pits, 5=lateral laminae, 6=pinwheel domatia, 7=petiolar flap, 8=coalesced veins, 10=multiple types of domatia or hybrid form.

Species	Domatia presence	Domatia type
Blakea acostae	0	0
Blakea acuminata	1	2
Blakea adscendens	0	0
Blakea aeruginosa	0	0
Blakea albertiae	0	0
Blakea allotricha	0	0
Blakea alternifolia	1	2
Blakea amabilis	0	0
Blakea amplifolia	0	0
Blakea andreana	0	0
Blakea anisophylla	0	0
Blakea anomala	0	0
Blakea arboricola	0	0
Blakea argentea	0	0
Blakea asplundii	0	0
Blakea attenboroughii	0	0
Blakea austin-smithii	1	7
Blakea barbata	0	0
Blakea bocatorena	0	0
Blakea brachyura	0	0
Blakea bracteata	1	2
Blakea brasiliensis	0	0
Blakea brenesii	0	0
Blakea brevibractea	0	0
Blakea brunnea	0	0
Blakea bullata	0	0
Blakea calcarata	1	1
Blakea calophylla	0	0
Blakea calycosa	0	0
Blakea calycularis	1	8
Blakea calyptrata	0	0
Blakea campii	1	6
Blakea castanedae	0	0
Blakea chlorantha	1	7
Blakea ciliata	1	8
Blakea clavata	1	8
Blakea clusiifolia	0	0
Blakea coloradensis	0	0

Blakea cordata	0	0
Blakea costaricensis	0	0
Blakea crassifolia	0	0
Blakea crinita	0	0
Blakea cuatrecasasii	0	0
Blakea cuneata	0	0
Blakea cuprina	0	0
Blakea cutucuensis	1	1
Blakea darcyana	0	0
Blakea dimorphophylla	0	0
Blakea discolor	1	1
Blakea dodsoniorum	1	10
Blakea droseropila	1	2
Blakea durandiana	0	0
Blakea echinata	0	0
Blakea elliptica	0	0
Blakea eplingii	0	0
Blakea eriocalyx	1	8
Blakea fasciculata	0	0
Blakea ferruginea	0	0
Blakea fissicalyx	0	0
Blakea florifera	0	0
Blakea foliacea	1	4
Blakea formicaria	0	0
Blakea fragrantissima	0	0
Blakea fuchsioides	0	0
Blakea gerardoana	0	0
Blakea glaberrima	0	0
Blakea glabrescens	0	0
Blakea glandulosa	0	0
Blakea gracilis	1	4
Blakea granatensis	0	0
Blakea grandiflora	0	0
Blakea gregii	0	0
Blakea grisebachii	0	0
Blakea guatemalensis	0	0
Blakea hammelii	0	0
Blakea hammettiorum	0	0
Blakea harlingii	0	0
Blakea henripittieri	1	2
Blakea herrerae	0	0
Blakea hexandra	0	0
Blakea hirsuta	1	8

Blakea hirsutissima	0	0
Blakea hispida	0	0
Blakea holtonii	0	0
Blakea horologica	1	2
Blakea hydraeformis	0	0
Blakea incompta	0	0
Blakea induta	0	0
Blakea inflata	1	10
Blakea insignis	1	1
Blakea intricata	0	0
Blakea involvens	1	8
Blakea jativae	0	0
Blakea killipii	0	0
Blakea laevigata	0	0
Blakea lanuginosa	0	0
Blakea latifolia	1	8
Blakea lentii	0	0
Blakea lindeniana	0	0
Blakea litoralis	1	4
Blakea longibracteata	0	0
Blakea longiloba	0	0
Blakea longipes	0	0
Blakea longisepala	0	0
Blakea macbrydei	0	0
Blakea macrantha	0	0
Blakea madisonii	0	0
Blakea maguirei	0	0
Blakea maurofernandeziana	0	0
Blakea mcphersonii	0	0
Blakea megaphylla	0	0
Blakea mexiae	0	0
Blakea micrantha	0	0
Blakea modica	0	0
Blakea monticola	0	0
Blakea mortoniana	0	0
Blakea multiflora	1	1
Blakea muricata	0	0
Blakea nangaritzana	0	0
Blakea nareliana	0	0
Blakea nodosa	0	0
Blakea oldemanii	1	2
Blakea orientalis	0	0
Blakea ovalis	0	0

Blakea paleacea	0	0
Blakea paludosa	0	0
Blakea paniculata	0	0
Blakea parasitica	0	0
Blakea parvifolia	1	4
Blakea pascoensis	0	0
Blakea pauciflora	1	4
Blakea pectinata	0	0
Blakea penduliflora	0	0
Blakea perforata	0	0
Blakea pichinchensis	0	0
Blakea pilosa	0	0
Blakea platypoda	0	0
Blakea pluvialis	0	0
Blakea podagrica	1	2
Blakea polyantha	0	0
Blakea portentosa	0	0
Blakea princeps	0	0
Blakea pulverulenta	1	2
Blakea punctulata	1	2
Blakea purpusii	0	0
Blakea pyxidanthus	1	10
Blakea quadrangularis	1	10
Blakea quadriflora	1	5
Blakea repens	0	0
Blakea ricardoi	0	0
Blakea rosea	0	0
Blakea rostrata	0	0
Blakea rotundifolia	1	8
Blakea rupicola	0	0
Blakea sawadae	0	0
Blakea scarlatina	0	0
Blakea schlimii	1	10
Blakea schultzei	0	0
Blakea sessilifolia	0	0
Blakea setosa	0	0
Blakea spadiciflora	0	0
Blakea spruceana	1	10
Blakea squamigera	0	0
Blakea standleyana	1	8
Blakea standleyi	0	0
Blakea stellaris	0	0
Blakea stephanochaeta	1	1

Blakea steyermarkii	0	0
Blakea stipulacea	0	0
Blakea storkii	0	0
Blakea suaveolens	0	0
Blakea subbarbata	1	10
Blakea subconnata	1	2
Blakea subpanduriformis	0	0
Blakea subscabrula	0	0
Blakea subsessiliflora	0	0
Blakea subvaginata	1	2
Blakea superba	1	10
Blakea tapantiana	0	0
Blakea tetramera	0	0
Blakea tetroici	0	0
Blakea toachiensis	0	0
Blakea trianae	0	0
Blakea trinervia	1	1
Blakea truncata	0	0
Blakea tuberculata	0	0
Blakea turbinata	0	0
Blakea unguiculata	0	0
Blakea urbaniana	0	0
Blakea vallensis	1	1
Blakea venusta	0	0
Blakea verrucosa	0	0
Blakea villosa	0	0
Blakea warszewicziana	0	0
Blakea watsonii	0	0
Blakea wilburiana	0	0
Blakea wilsoniorum	0	0
Chalybea brevipedunculata	1	6
Chalybea calyptrata	1	6
Chalybea corymbifera	1	6
Chalybea ecuadorensis	1	6
Chalybea kirkbridei	1	6
Chalybea macrocarpa	1	6
Chalybea minor	1	6
Chalybea mutisiana	1	6
Chalybea occidentalis	1	6
Chalybea penduliflora	0	0
Chalybea peruviana	1	6

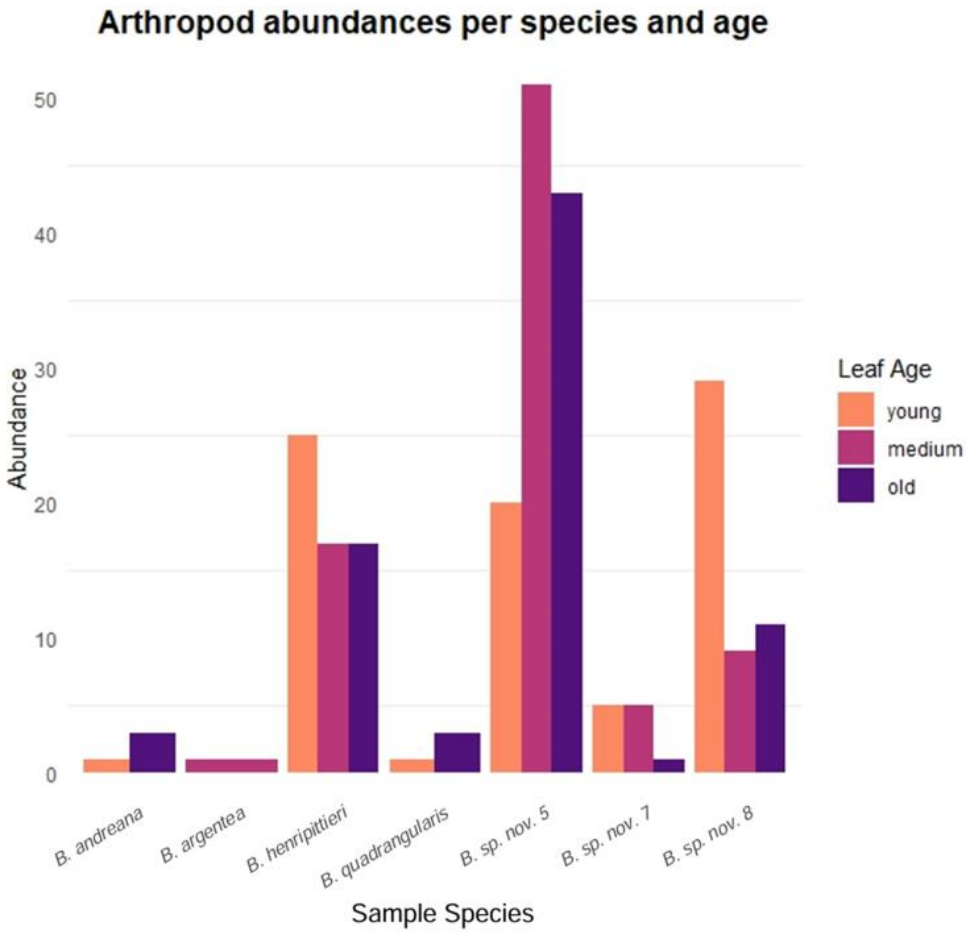
A 2. Table of pairwise change rates from one to another domatia type or loss, calculated by stochastic character mapping with multiple characters. 0=domatia absent, 1=hair tufts, 2=marsupiform pocket, 4=recessed pits, 5=lateral laminae, 6=pinwheel domatia, 7=petiolar flap, 8=coalesced veins, 10=multiple types of domatia or hybrid form. The root likelihoods for the different types from the ancestral character estimation are shown below.

	0	**1**	**2**	**4**	**5**	**6**	**7**	**8**	**10**
0	-	4.42	5.02	2.32	1.05	0.73	2.07	4.63	4.8
1	0.5	-	0.21	0.08	0.03	0.13	0.06	0.29	0.66
2	1.68	0.19	-	0.07	0.34	0.17	0.11	1.16	0.4
4	2.2	0.17	0.18	-	0.15	0.2	0.07	0.17	0.13
5	0.32	0.12	0.47	0.05	-	0.11	0.06	0.14	0.18
6	0.35	0.14	0.14	0.1	0.11	-	0.02	0.15	0.19
7	0.65	0.14	0.15	0.07	0.09	0.11	-	0.13	0.18
8	0.4	0.14	0.15	0.09	0.09	0.15	0.04	-	0.15
10	0.32	0.42	0.33	0.08	0.06	0.15	0.06	0.14	-
Root likelihoods	**0**	**1**	**2**	**4**	**5**	**6**	**7**	**8**	**10**
	0.349	0.071	0.071	0.072	0.071	0.151	0.071	0.071	0.071

A 3. Table of all *Blakea* species I sampled in the field and where I found them. I encoded Domatia types as 0=no domatia, 1=hair tufts, 2=marsupiform pockets, 8=coalesced veins. Coordinates are in D° M' S" format.

Species	**Individual**	**Domatia Type**	**Coordinates**	**Elevation [m]**	**Locality**
Blakea andreana	1	0	6°47'19.0"N, 76°17'01.5"W	2050	Reserva El Tambo, Nutibara, Antioquía
Blakea argentea	1	0	5°39'06.5"N 75°45'49.9"W	2600	Reserva El Globo, Támesis, Antioquía
Blakea henripittieri	1	2	4°44'55"N, 76°17'27"W	2150	Reserva Natural Cerro El Inglés, camino al límite con Chocó, Valle de Cauca, Dagua
Blakea henripittieri	2	2	4°44'55"N, 76°17'27"W	2150	Reserva Natural Cerro El Inglés, camino al límite con Chocó, Valle de Cauca, Dagua
Blakea henripittieri	3	2	3°31'59"N, 76°45'11"W	1210	Alrededores del punto de avistamiento de aves Doña Dora, Vereda El Queremal, Valle de Cauca, Dagua
Blakea quadrangularis	1	1	5°39'08.6"N, 75°45'49.6"W	2600	Reserva El Globo, Támesis, Antioquía
Blakea quadrangularis	2	1	5°39'09.0"N 75°45'50.0"W	2600	Reserva El Globo, Támesis, Antioquía
Blakea quadrangularis	3	1	5°39'09.0"N 75°45'50.0"W	2600	Reserva El Globo, Támesis, Antioquía
Blakea quadrangularis	4	1	5°47'42.5"N 76°04'06.4"W	1420	Camino de La Mina al Monte Blanco, Ciudad Bolivar, Antioquía

Blakea quadrangularis	5	1	5°47'42.5"N 76°04'06.4"W	1420	Camino de La Mina al Monte Blanco, Ciudad Bolivar, Antioquía
Blakea podagrica	1	2	3°31'59"N, 76°45'11"W	1210	Alrededores del punto de avistamiento de aves Doña Dora, Vereda El Queremal, Valle de Cauca, Dagua
Blakea sp. nov. 5	1	8	6°47'43"N, 76°17'38"W	2220	Reserva El Tambo, Nutibara, Antioquía
Blakea sp. nov. 5	2	8	6°47'16.5"N, 76°17'20.7"W	2200	Reserva El Tambo, Nutibara, Antioquía
Blakea sp. nov. 5	3	8	6°46'57"N, 76°16'54"W	2200	Reserva El Tambo, Nutibara, Antioquía
Blakea sp. nov. 7	1	8	4°45'01.0"N, 76°17'27.7"W	2100	Reserva Natural Cerro El Inglés, camino al límite con Chocó, El Cairo, Valle de Cauca, Dagua
Blakea sp. nov. 8	1	8	3°32'37"N, 76°43'42"W	1620	Camino al acueducto veredal, Vereda El Queremal, Valle de Cauca, Dagua
Blakea sp. nov. 8	2	8	3°32'37"N, 76°43'42"W	1620	Camino al acueducto veredal, Vereda El Queremal, Valle de Cauca, Dagua



A 4. Abundance of arthropods per leaf age and species.