Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in
Plant Biology

Diversity and development of domatia: Symbiotic plant structures to host mutualistic ants or mites

Guillaume Chomicki[1,a], Nathanael Walker–Hale[1,a],
J. Peter Etchells[1], Eleanore J. Ritter[2] and Marjorie G. Weber[3]

Across the tree of life, specialized structures that offer nesting sites to ants or mites – known as domatia – have evolved independently hundreds of times, facilitating ecologically important defence and/or nutritional mutualisms. Domatia show remarkable diversity in morphology and developmental origin. Here we review the morpho-anatomical diversity of domatia, aiming to unveil the primary mechanisms governing their development. We propose hypotheses to explain the formation of these structures, based on anatomical studies of domatia and developmental genetic analyses in model species. While genes involved in domatium formation are so far unknown, domatia appear to originate via spatiotemporal shifts in the expression of common developmental genetic pathways. Our review paves the way to the genetic dissection of domatium development.

Addresses
[1] Department of Biosciences, Durham University, South Rd, Durham, DH1 3LE, UK
[2] Department of Plant Biology, Michigan State University, Wilson Rd, East Lansing, MI, 48824-6406, USA
[3] Department of Ecology and Evolutionary Biology, University of Michigan, 3034 Biological Sciences Building 1105 North University Ave., Ann Arbor, MI, 48109-1085, USA

Corresponding author: Chomicki, Guillaume (guillaume.chomicki@durham.ac.uk)
[a] These authors contributed equally.

Current Opinion in Plant Biology 2024, **82:**102647

This review comes from a themed issue on **Growth and development 2024**

Edited by **Madelaine Bartlett** and **Annis Richardson**

For a complete overview see the Issue and the Editorial

Available online xxx

https://doi.org/10.1016/j.pbi.2024.102647

Keywords
Domatia development, ant domatia, mite domatia, domatia diversity, domatia evolution.

Introduction

Many plant species rely on arthropods for defence. These ‘indirect defences’ rely on mutualisms in which plants are protected by arthropods in return for rewards provided by the plant [1,2]. One reward that has evolved hundreds of times across plants are domatia — nesting sites for ant or mite symbioses [2]. Ant domatia have evolved about 160 times in plants, with ∼700 ant-plant species across the plant tree of life [2, Box 1, Figure 1], and thousands of plant species have leaf domatia that host mites [3,4, Box 1, Figure 2]. Ant domatia evolved later than mite domatia: molecular clock dating analyses suggest that ant-plant symbioses involving domatia are no older than the Miocene (15—20 Myrs; [2]), while the fossil record dates ant-mite symbiosis to at least the late Cretaceous (75 Myrs, [5]). In this review, we focus on the development of both ant and mite domatia and its relevance as emerging systems in the genetics of mutualism.

Despite their ecological importance, the study of domatia development is still in its infancy. Domatia are constitutive morphogenetic structures that develop even in the absence of insect occupants. Domatia vary enormously in their morphology, structure, size, complexity, and organ modification (Figs. 1, 2, Box 1). The formation of domatia has been studied in only a small number of species, and synthesising these studies can illuminate commonalities and differences in domatia development and generate testable hypotheses regarding their developmental genetic basis. To this end, we review research on the development of domatia, highlighting promising systems to study their molecular genetic underpinnings. In each section, we highlight the morphogenetic processes when they are known, and connect them to potential developmental pathways based on similarity to developmental patterns in model species. We suggest that despite their structural diversity, domatia may have coopted existing regulatory pathways and draw on conserved developmental programs, and considering these pathways suggests promising candidates for developmental study. Our review paves the way for an evo-devo approach to dissect the development of these unique mutualistic structures, which will shed light on their repeated evolution and facilitate manipulating these important ecological interactions for plant improvement.

Onset of domatia formation

Timing of domatia development is crucial to their role in ecological interactions. Insect partners have to re-

Box 1. The diversity of domatia

Ant domatia

Ant domatia require both a hollow interior and openings for ant entry. Openings may be: (i) pierced by ants (e.g., *Barteria fistulosa* [Passifloraceae]); (ii) eased by prostoma, a tissue thinning that facilitates entry, typically opened by ant founder queens when colonizing young ant-plants (e.g., *Cecropia*); or (iii) fully formed by the plant (e.g., *Leonardoxa*). Ant domatia exhibit significant morphological diversity, that can be broadly categorized into seven types. First, stem domatia. These include hollow stems or twigs, ranging from a few swollen internodes (e.g., *Humboldtia brunonis* [6]) to the entire primary stem (e.g., *Cecropia* [7]) (Figure 1a). Second, leaf pouch domatia. These vary from whole-leaf pouches (e.g., *Dischidia*) to smaller pouches within leaves, as seen in *Tococa* (Melastomataceae) (Figure 1b) and *Tachigali* [8], where pouches derive from the rachis of composite leaves. Third, leaf base domatia, involving cavities formed within interlocking leaf bases, as in *Tillandsia*. Fourth, stipular domatia, which include the famous ant-acacias in Central America (Figure 1c) and Africa. Other forms involve fused stipules (ocrea, Figure 1e), either partially or fully closed, as in some rattan palms (Figure 1d). Fifth, root domatia. These feature hollow root tubers or complex 3D root networks used by ants for nesting, as seen in *Coryanthes* orchids. Sixth, external domatia. These include epiphytic species with flattened leaves (e.g., *Hoya imbricata*, Figure 1e) or stems (e.g., *Lecanopteris mirabilis*), forming sturdy nesting sites against tree bark. And finally, hypocotyl domatia: A unique adaptation in epiphytic Rubiaceae (Hydnophytinae) (Figure 1f–g) [9-11**]. Ant domatia vary in occupancy, with some species being specialists (occupied by a single ant species), while others are generalists, hosting multiple species.

Mite domatia

Mite domatia manifest primarily in three distinct forms: tuft, cave (also called “pocket”), and pit domatia (Figure 2a). All three forms typically appear in the vein axils on the underside of plant leaves where a depression in the leaf surface forms a home for mites and their eggs. In tuft domatia, the depression in the leaf surface is covered by a dense layer of trichomes, whereas in cave domatia, an open flap of laminar tissue covers the depression, and in pit domatia, a closed layer of laminar tissue with a small pore for mite access is present (Figure 2a). Gradations between these forms exist. For example, trichomes are often present within pit and pocket domatia, and some tuft domatia form a ring of hairs surrounding a central cavity devoid of trichomes. These morphologies collectively facilitate the formation of semi-enclosed chambers, which serve as habitats for various stages of mite life cycles.

Phylogenetic diversity of domatia

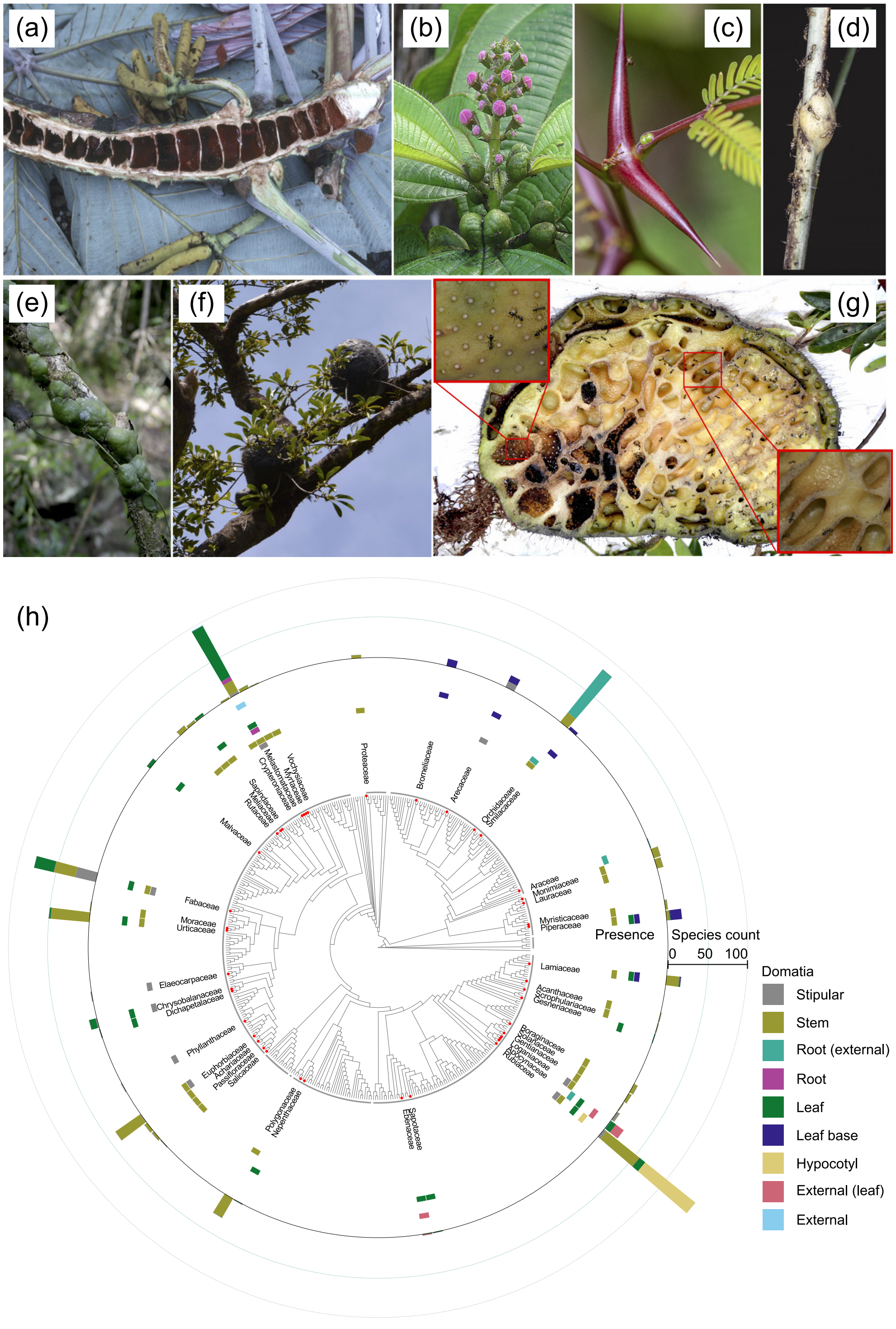
Both ant and mite domatia show considerably broad disparities in their phylogenetic distributions across the angiosperm tree (Figure 1h, Figure 2a), both within and between domatia types. On the one hand, widespread convergent origins of domatia may suggest that their development depends on conserved pathways; on the other hand, paucity of domatia in some lineages may suggest significant constraints on their development and evolution. Presence of stipular thorns, palmate leaf venation, and a minimal threshold of stem diameter have been suggested to facilitate ant domatia evolution [2], while availability of mutualist partners is also likely to ultimately drive domatia origins and loss [9]. Mite domatia are more common (Figure 2b); the developmental modifications required for their evolution may be less complex.

assemble at each generation, and later onset can imply long periods of time without the benefit of the mutualist. Unsurprisingly then, in most plants with ant-domatia, these structures develop early in ontogeny, in the seedling (e.g. hypocotyl domatia: Hydnophytinae [9-11**]; leaf domatia: *Callicarpa* [12*], *Hirtella*, *Maieta*, and *Tococa* [13]) or the sapling (e.g. stem domatia: *Cecropia* [14] and *Macaranga* [15]), but most feature some early leaves or internodes without domatia. In stem domatia, there is a minimum size below which ants cannot inhabit the stem, and in hollow-stemmed species, there is a minimum ratio of thickness required to support a given leaf area, which requires young plants to invest in additional stem thickening to support occupancy by ants [16*,17]. Thus, development of domatia early in ontogeny is costly and stem domatia may first have formed during later stages [16*-19]. Some specialised species with stem domatia likely evolved to form earlier in development [16*].

Genetic control of onset is largely unknown, but in some domatium-bearing trees or large shrubs, the production of domatia appears to be coupled with phase change. Detailed work on the Central American ant-acacias [20**] has revealed that the timing of formation of ant-acacia (*Vachellia corniger* and *V. collinsii*) domatia after the first 5 nodes is likely to be regulated by microRNAs and their targets: the miR156/157-SPL vegetative-phase change pathway. This pathway features a predictable decline in the microRNAs miR156 and miR157, coupled with a corresponding increase in expression of their targets — the *Squamosa Promoter Binding Protein-Like* (*SPL*) transcription factors (TFs). This pathway is pivotal in mediating juvenile to adult phase changes in *Arabidopsis* [21]. Interestingly, ant-acacia extrafloral nectaries and protein-rich food bodies known as beltian bodies, which deliver the food rewards crucial to the ant-acacia mutualism, are also formed following the miR156/157 decline. This suggests that the syndrome may have arisen through the co-option of a pre-existing, age-dependent genetic mechanism [20**]. This supports the idea that domatia evolved by co-option of existing genetic regulation, but the downstream targets of miRNA156/157-SPL pathway may be novel developmental candidates, and the genetic pathways involved in acacia domatia development are so far unknown. This suggests that the same pathway may be responsible for transitions between domatia-less and domatia-bearing leaves and stems in other species, and a key experiment will be to characterise transcriptomic changes in leaves during the onset of domatia, for example in *Callicarpa saccata*, where leaves from the first two nodes do not form domatia [12*].

Mite domatia also form early in plant development and can even be present on the earliest emerging leaves of saplings [4], suggesting that genetic control of their onset may be distinct from those controlling ant domatia. Timing of mite domatia development on leaves

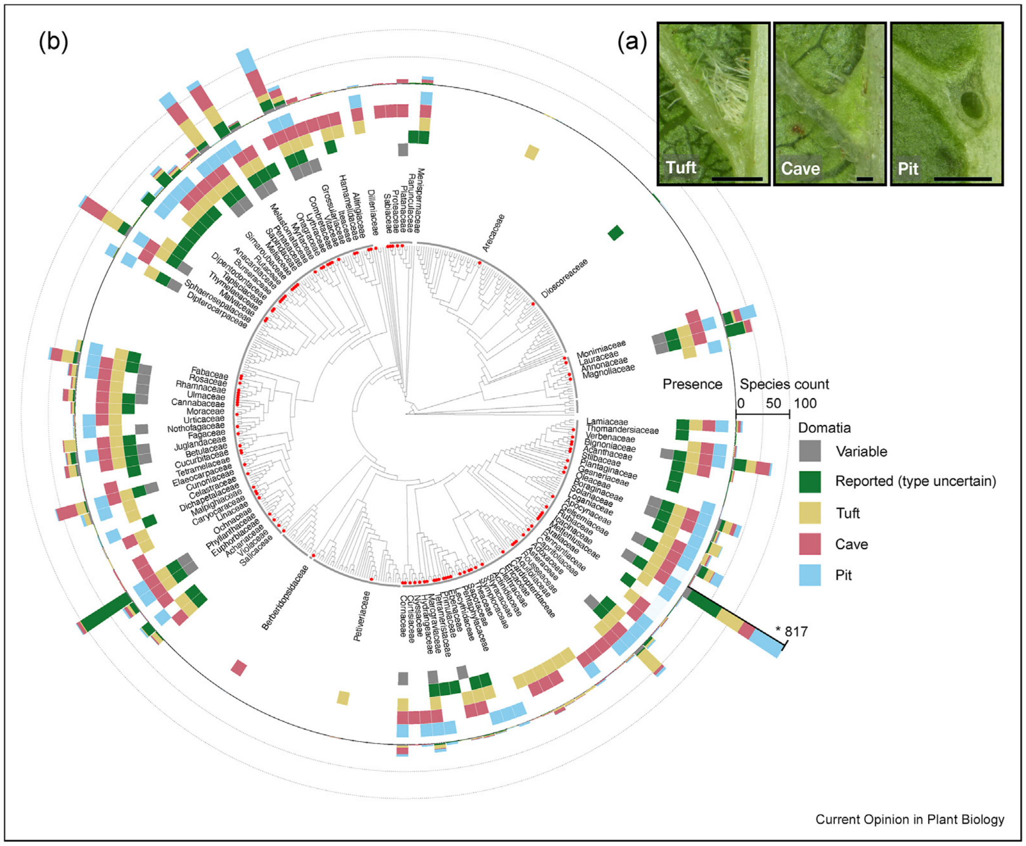
Figure 1



Current Opinion in Plant Biology

Morphological diversity and phylogenetic distribution of ant domatia. (**a-f**) Ant domatia arose from a variety of developmental origins. (a) Stem domatia: *Cecropia* sp. (Urticaceae). (**b**) leaf pouch domatia: *Tococa guianensis* (Melastomataceae). (**c**) Stipular thorn domatia: *Vachellia cornigera* (Fabaceae). (**d**) Ocrea (fused stipules) domatia: *Korthalsia rostrata*. (**e**) External (leaf) domatia: *Hoya imbricata* (Apocynaceae). (**f–g**) Hypocotyl domatia: *Squamellaria wilsonii*, (**f**) shows a longitudinal section of the domatium, highlighting the patterned network of cavities that develops constitutively even in the absence of ants. The top left inset shows the detail of the warty absorptive walls where ants defecate, and the bottom right inset shows the smooth walls where ants rear their brood. (**g**) Phylogenetic distribution of ant domatia types (see Box 1 for description). The inner circle shows the presence of

Figure 2



Current Opinion in Plant Biology

Morphological diversity and phylogenetic distribution of mite domatia. (**a**) The three types of mite domatia: *Vitis riparia* (tuft), *Ampelopsis brevipedunculata* (cave), *Coffea arabica* (pit). Scale bar = 1 mm. (**b**) Phylogenetic distribution of mite domatia types (see Box 1 for description). The inner circle shows the presence of domatia types in the flowering plant tree of life, and the outer circle shows the species count for each domatia type and family. The category 'Reported – type uncertain' refers to species for which mite domatia are reported but the type has not been specified, and the category variable refers to species that can have more than one type of mite domatia. Photographic credit: A. Myers. See supplementary dataset S2 for the list of plants with mite domatia used to make the phylogenetic distribution shown in (**b**). Tree from Ref. [89] reduced to family-level sampling and plotted with ggtree [90] in R v4.3.3 [91]. Data from dataset S2 comes from [3].

varies among taxa, but invagination and depression of the leaf surface and formation of the chamber covering begins while leaves are still in bud [4,22].

Development of stem domatia

It is thought that some domatia-bearing mutualisms evolved in response to parasitism from scale insects [2]. Early stages in the evolution of stem domatia are thought to involve ants living in cavities that are either made by twig borers [23] which is common in the tropics [24], or in species that have hollow stems that ants pierce to attain the pith — thus being a preadaptation. Thicker twigs might also be more likely to be colonised, and lineages with thicker twigs concomitantly more likely to evolve domatia [16*]. An important insight arose from the study of what likely represents an early stage in the evolution of stem domatia in the tropical tree *Vochysia vismiaefolia* [25*]. While ant-plants develop domatia constitutively, here they are induced by ants, which bite holes in the internodes of soft twig apices and hollow out the pith. Mechanically mimicking ant drilling led to a ∼30% enlargement in twig diameter [25*]. This finding suggests that a physiological response to mechanical stress, potentially involving wound-induced pathways such as those mediated by jasmonic acid or ethylene hormones, may contribute to initiation of domatia formation [26,27]. In support of this hypothesis, both jasmonic acid and ethylene has

domatia types in the flowering plant tree of life, and the outer circle shows the species count for each domatia type and family. Photographic credit: (**a**): J. Longino. (**b**): D. Culbert. (**c**): E.P. Mallory. (**d**): T. Rodd. (**e**) W.J. Baker. (**f–g**): G. Chomicki. See Supplementary dataset S1 for the list of plants with ant domatia (updated from Chomicki (2019)), used to build the phylogenetic distribution shown in (g). Tree from Ref. [89] reduced to family-level sampling and plotted with ggtree [90] in R v4.3.3 [91].

been demonstrated to promote radial stem growth [28–30]. While the exact genetic and hormonal mechanisms remain to be elucidated, induction of enlarged stem by ant drilling may represent an early stage in the evolution of stem domatia. Comparison of the phylogenetic distribution of ant boring in plants relative to that of stem domatia would be a promising approach to test this hypothesis.

Stem domatia develop via several mechanisms. The entrance holes are often preformed (prostoma as in *Cecropia*, Box 1), with weak tissue patches being destroyed by the founding queen that first colonizes the domatium. While the formation of the hollow space involves the removal of soft pith by ants in some species (for example in unspecialized *Macaranga hosei* [31]), in others it appears to be primarily driven by cell death (lysogeny), for example in genera enriched in species with stem domatia, such as *Cecropia* and *Macaranga* [15], and to a lower extent local alteration of cell separation (schizogeny), as in *Humboldtia brunonis* [6]. It seems likely that regional differences in growth also play a role, especially in those groups where domatia are only one to few internodes long and bulged (e.g. *Leonardoxa*, *Cordia*, and *Triplaris*), but this remains unstudied.

In the genus *Piper*, the development of ant-inhabited stem domatia exhibits remarkable diversity, driven by different mechanisms. In species like *P. immutatum* and *P. pterocladum*, domatia are lysigenous, forming from the disintegration of cells within the stem, a few millimeters behind the apical meristem [32*]. This contrasts with Central American ant-plants in *Piper* section *Macrostachys*, where domatia develop through ant excavation of solid stems [33], revealing that domatia can evolve by divergent pathways even in closely related species. Specifically, in the section *Macrostachys*, species have heterogeneous pith with large cells devoid of intracellular crystals and small peripheral cells rich in oxalate crystals [32*]. Ants exclusively excavate the large, crystal-free cells [32*]. The entrance holes in *P. immutatum* are created via apoptotic processes, whereas in *P. pterocladum*, they vary in position and are excavated by ants in the leaf axil [32*]. In *P. immutatum* and *P. pterocladum*, lining cells of the cavity remain undifferentiated, facilitating the later production of food rewards (pearl bodies) inside the domatia [32*]. Developmentally, genes regulating programmed cell death and repression of differentiation might be pivotal in lysigenous cavity formation. By contrast, in section *Macrostachys*, cavities develop a lining of wound-response tissue following ant excavation. This tissue, originating from pith cells, undergoes periclinal divisions and becomes suberized, forming a protective layer [33]. Periclinal divisions and deposition of suberin are characteristics of periderm formation [34], a process under the control of auxin and downstream TFs *Wuschel-Related Homeobox 4* and *Brevipedicellus (BP)* in *Arabidopsis* [35], suggesting that auxin pathways could be involved in the formation and maintenance of these structures. A key experiment would be to compare pith cell transcriptomes between stems before and after excavation by ants, to identify candidates regulating cell division and suberin production in this context.

Development of leaf domatia

Leaf domatia involving pouch-like structures have evolved convergently in many flowering plant families, including Apocynaceae, Chrysobalanceae, Gesneriaceae, Lamiaceae, Malvaceae, Melastomataceae, Rubiaceae, and Sapotaceae (Figure 1). Leaf domatia in Apocynaceae are unique in involving the whole leaf. The development of leaf domatia appears to be primarily driven by regional differences in growth [12*,36-38]. Cell separation probably often occurs at the onset to generate an empty space that is then enlarged via differential growth and cell death might be involved in some species in the formation of the entrance hole.

Leaf domatia that involve pouches have been described as developing in two distinct ways: from a curling blade at the base of the lamina [36,37], or from warping outward growth from an area at the junction between the leaf blade and the petiole [12*,38]. The former mode was described in *Hirtella physophora* (Chrysobalanaceae), where the lamina curls under the blade near the petiole, creating an intermediate structure that is open at the margins [36,37]. This transitional structure then closes on later leaves [36,37]. This curling blade could result from cell division and growth at lamina margins, or from differential growth across the surface of the domatium [12*]. A detailed anatomical study of two distantly related ant-plants: *C. saccata* (Lamiaceae) from Borneo and *Tococa guianensis* (Melastomataceae) from the Neotropics revealed that leaf pouch domatia forms according to the ‘warping’ hypothesis, from 3D outward growth of the lamina caused by high levels of cell proliferation at the distal end of the domatia near the blade/petiole boundary, creating a structure that is closed at the proximal end; entrance holes occur on the abaxial side, close to the midvein (Figure 2, [12*,38]). *C. saccata* can also show a transitional leaf with open developing domatia, reinforcing their formation by distortion of the leaf lamina [12*]. In other species like *Maieta guianensis* and *T. guianensis*, the transition between domatia-less and domatia bearing leaves is abrupt [13*,37].

Another form of leaf domatia are the pits, pockets, and caves in abaxial vein axils that constitute mite domatia. There have been very few studies on the development and genetics of mite domatia. However, several anatomical studies point to delayed cell differentiation of mesophyll cells in early leaf development driving chamber formation [22,39–41]. The resulting depressed cavity in the leaf is common to all mite domatia types. Moreover, some species can exhibit multiple morphologies of mite domatia on the same leaf (e.g. *Viburnum odoratissimum*, M.G. Weber, pers. Obs.), suggesting that common genetic pathways may act on the early stages of development. Nishida et al. [22] used detailed histology to investigate the development of mite domatia in *Cinnamomum camphora* and found that cavity formation resulted from a difference in growth rate between the upper and lower part of the lamina, whereby the lower mesophyll and lower epidermal cells divide faster than the upper mesophyll or epidermal cells leading to a leaf depression at the domatia site. Delayed timing of cell differentiation in the mesophyll compared to control tissue was also observed [39,40]. However, other features of mite domatia development appear less consistent across species. Histological examination of the mite domatia in 27 Australasian plants species revealed variability in the thickness of epidermal cells in domatia compared to control laminar tissue, as well as variation in the presence of structural reinforcement (e.g., in the form of thick-walled subepidermal cells lining the domatia chamber in *Endiandra cowleyana* or reinforcing collenchyma in *C. camphora*) [41]. Detailed comparative studies of mite domatia across species are rare, making it challenging to draw conclusions on the anatomical similarities and differences across mite domatia types; further detailed examinations are needed (Box 2).

The above examples suggest that out-of-plane deformations are key features of leaf domatia formation for both ant and mite domatia. Theoretical and empirical work suggest that out-of-plane deformations can be generated by differences in the rate and/or orientation of growth in adjacent tissue layers or zones, for example between adaxial and abaxial leaf domains [42**,43]. Developmental patterns in *C. saccata* and *T. guianensis* are reminiscent of the *Blade-On-Petiole1 and 2* mutants *BOP1 and BOP2* in *Arabidopsis* [44,45]. *BOP1 and 2* repress the expression of the meristem-determining genes *class I KNOX*, *Shootmeristemless* (*STM*), *Bp*, and *Knotted-Like From Arabidopsis Thaliana2* (*KNAT2*) in *Arabidopsis* leaves [44] by activating Asymmetric Leaves 2 (AS2; [45]), which directly binds to *KNOX1* promoters as an AS1-AS2 protein dimer [46,47]. Consequently, *BOP* mutant

Box 2. Grapevine as an emerging model for mite domatia genetics

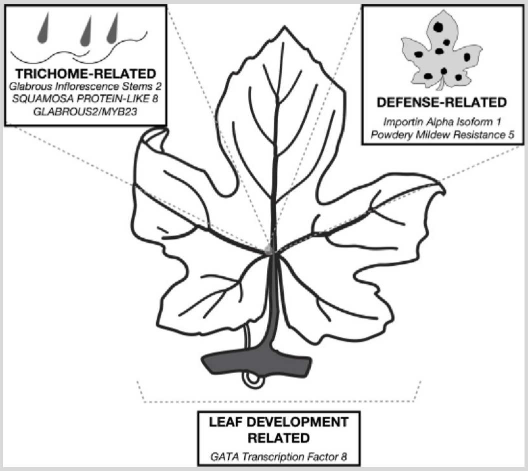
Recent studies on the genetic basis of tuft domatia have positioned grapevine (*Vitis*) as a model for investigating mite domatia development. These findings highlight several genetic pathways involved in this process (Figure 3).

First, candidate genes related to trichome development are implicated in the dense clusters of trichomes at vein axils that form tuft domatia. These include genes encoding TFs like the C_2H_2 zinc finger proteins *Glabrous Inflorescence Stems 2*, *Squamosa Protein-Like 8* (*SPL8*), gene regulating gibberellin-mediated processes, including trichome density [79], and the Myb protein domain *GLABROUS2/ MYB23* [77*,78*]. Given their roles in other systems, these TFs likely influence not only the development but also the size and density of tuft domatia hairs [80].

Second, VvGATA8, a strong candidate gene associated with domatia density [78*], is homologous to a gene in *Arabidopsis* that regulates leaf shape [81]. The genetic link between leaf shape and trichome density in *Vitis* [82] suggests a possible co-option of leaf developmental pathways for trichome/domatia development, though the exact mechanism remains unclear.

Third, genes involved in fungal pathogen responses, specifically *Importin Alpha Isoform 1* and *Powdery Mildew Resistance 5*, are also implicated in domatia development [78*]. Although domatia play a crucial role in powdery mildew defence in *Vitis* [83], the connection between these defence-related genes and domatia development is not fully understood. It is possible that there is a tradeoff between direct fungal defence and indirect domatia-mediated defence, but further research is needed. Such tradeoffs between biotic and abiotic defence have been explored in plant ecology and evolution with mixed results [84–87]. In *Vitis*, the size of mite domatia is negatively correlated with the diversity of secondary metabolites across species [88], hinting at a tradeoff in defence strategies.

Figure 3



Grapevine (*Vitis vinifera*) as an emerging model for mite domatia genetics. Quantitative trait loci and genome-wide association studies reveal three main functional pathways associated with the development, size and spacing of mite tuft domatia.

petioles retain some meristem identity and thus the ability to initiate new tissue. Similar retention of meristematic identity in lateral organs has been shown to result in cup-shaped growth, for example in dominant *Hirzina* and *Invaginata* mutants in *Antirrhinum* petals [48]. Furthermore, *BOP2* is thought to activate *KNAT6* in *Arabidopsis* [49], a gene related to *STM*, *BP*, *KNAT2*, *HIRZ*, and *INA*. *KNAT6* regulates the boundary between meristem and lateral organs [50]. Moreover, *AS2*, a direct transcriptional target of BOP protein [45] is an adaxial/abaxial patterning determinant in leaves [51]. Work in the aquatic carnivorous plant *Utricularia gibba* (Lentibulariaceae), shows that shifts from planar to 3D cup-shaped growth can be achieved by a shift in the expression of abaxializing and adaxializing genes and their effects on growth [42**]. Thus, it is possible that changing the dorsiventral identity at the basal ends of the leaf might generate a 3D saccate growth as a domatia. In *C. saccata*, cell division is concentrated at the distal end of the domatia, suggesting that cell division periclinal to the blade petiole margin may be followed by growth in more proximal cells creating a rounded dome [12*], ('areal conflict' [43]). Similarly detailed information is not available for *H. physophora* or *T. guianensis*, but it is possible that the curling blade of the former is also explained by differential division and growth between abaxial and adaxial domains ('surface conflict' [43]), that is oriented longitudinally [12*], in which case curling and warping merely describe two different orientations of similar developmental process; detailed time courses of domatia development on a single leaf are necessary to determine this. On the other hand, if the 'curling blade' results from leaflet-like growth at the leaf margin, then regulators that influence leaf serrations and leaflet formation might be important for domatia development. *CUC* genes are negative regulators of leaf margin growth [52,53]. Local activation of *CUC* genes — and their negative regulator microRNA 164 — plays an important role in the formation of serrated leaf margins with each outgrowth involving relaxation of *CUC* repression [54]. Thus, in the curling blade scenario, which appears to hold for *H. physophora* [37], the *CUC*/miR164 pathway may be a good candidate for generating leaflets, and subsequently leaflet curling by differential growth to form the domatium tissue. Support for this hypothesis comes in part from analysis of members of the Cincinnata (CIN) group of the Teosinte Branched1/Cycloidea/Proliferating cell factor family of helix-loop-helix TFs. Dramatic leaf or leaflet curling is observed when *CIN* genes are absent, or when dominant negative forms are present, in *Antirrhinum*, *Arabidopsis*, *Cyclamen*, and *Rosa* [55–57]. The TCP3 CIN protein binds to the miRNA165a promoter in *Arabidopsis*, regulating its expression, and in turn, that of CUC genes [58]. Therefore, various genes involved in specifying meristem identity, organ boundary formation, adaxial/abaxial patterning, and differential growth could control the tissue deformations required for domatia formation. Melastomataceae is enriched with species forming leaf domatia (Figure 1b) and represents a promising system for research in domatium development. The genus *Tococa* alone features 32 domatium-bearing species [59], including species in which the domatia only develops in one of two leaves per pair. This asymmetry in domatia expression provides a controlled comparative framework, ideal for the molecular dissection and identification of genes mediating domatium formation. Observation of developmental series, microscopy of developing domatium sections [12*], and transcriptomic comparisons between common tissues in domatia-less and domatia-bearing leaves can reveal the developmental mode of leaf domatia.

Interestingly, the lamina structure of leaf domatia differ from the rest of the leaf in that it has lost the typical mesophyll differentiation into spongy and palisade mesophyll [12*,13*,37]. Instead, structural integrity of domatia is enhanced by cell wall modification, and domatia tissue show reduced chloroplast density, which implies reduced photosynthetic capacity [13*,37]. These data suggest that domatia evolution and development may involve a trade-off between mutualistic benefits and photosynthetic efficiency.

An interesting aspect of leaf domatium development occurs in *H. myrmecophila* where domatia are aborted from the leaves as they age. This strategy helps reduce ant presence in some branches — which is essential since an important ant partner of this species is *Allomerus octoarticulatus*, which castrates its host by cutting flowers. This abscission of leaf domatia is unique among myrmecophytes, and the physiological mechanism behind this domatia abortion is currently unknown [60]. Adaptive abscission has been reported in palms [61], and in general it is thought that the balance between auxin and ethylene drives its onset [62]. However, abscission requires an abscission zone: a region of small, dense cells enriched with plasmodesmata [63]. Abscission occurs via activation of a peptide ligand, IDA, which is perceived by HAESA and HAESA-like receptors. IDA-HAESA binding leads to activation of KNOX TFs which in turn promote the expression of cell wall degrading enzymes [64,65]. This phenomenon indicates that the evolution of domatia has integrated developmental mechanisms related to both complex shape formation and programmed organ removal.

Another type of leaf domatia are the inflated ocrea (leaf sheath appendages that might derive from modified stipules) that develop in some rattan species (Figure 1e). A micro-morphological study of the development of *Calamus longipinna* and relatives revealed that the ocrea forms axial plications that enable inflation that results in the domatia [66]. Importantly, this study revealed that three *Calamus* species, unlike two species of nonocreate palms, develop a unique leaf sheath extension that serves a preadaptation to the inflated ocreas in domatium-bearing rattans. Class I *KNOX* genes have been implicated in the development of plications in the palm *Elaeis guineensis* [67], but compound leaf development in the closely related palm *Chamaedorea elegans* was reportedly KNOX-independent [68], suggesting that alternative mechanisms may be involved in ocrea domatia development.

The most complex domatia: the hydnophytinae hypocotyl domatia

The Hydnophytinae is the largest clade of ant-plants, with ∼105 species in Australasia [9] They are epiphytic plants with domatia consisting of a modified hypocotyl that continues to grow throughout the plant's lifespan. Inside this swollen hypocotyl (which can reach ∼1 m in some species) is a network of interconnected cavities with entrance holes connected to the exterior. The structure of these varies, with specialized and obligate ant-plants having highly differentiated cavities, while generalist species have coarser, less differentiated cavities [11**]. The overall shape of the domatium develops by sustained differential growth in the hypocotyl, which continues throughout the plant's lifespan. Cavities form by lysogeny of small cell groups in areas experiencing active growth [69, 70], which means that the subsequent cell expansion and division then drives the expansion of these cavities. The development of the domatium follows two broad patterns: in generalist species, growth of the domatium occurs in a diffuse way, with new cavities added outwardly. In species with specialized symbioses with Dolichoderinae ants, the domatium grows apically, with new cavities added only in one direction [18,69]. This results in more reticulate cavities that have higher inner surface/volume ratio in specialized ant-plants [11**]. The mechanism mediating programmed cell death that leads to patterns is not entirely clear. A key element is that cavity walls become lined with phelloderm [69]. One possibility is that the phellogen forms first, producing a phelloderm (analogous to cork cambium) that isolates the cells from the rest of the parenchyma, which subsequently die [70]. Alternatively, programmed cell death may occur first, and the cavity could subsequently become lined with a suberised phelloderm. The first cavity emerges in seedlings and forms before the first entrance hole [71]. The position of this first entrance hole appears to be dependent upon gravity; plants artificially rotated to have their basal–apical axis horizontal developed entrance holes only on the lower side [71]. However in mature plants, a similar mechanism is less likely, as many species have very ordered and geometric patterns of entrance holes, while domatia can have many different orientations on trees (see e.g. Ref. [72]). The developmental genetics of hypocotyl domatia formation remains unknown, including the pathways contributing to hypocotyl swelling, determination of cell types involved in cavity formation, and spatial determination of cavity differentiation. Developmental series from germination of specialized and generalist species coupled with dissection and transcriptomic analysis of cavity forming tissue, and comparisons between basal and apical zones of the developing domatia, will help to suggest novel candidates or identify conserved regulators.

Domatia cavities have two types of inner walls: smooth walls impermeabilized by suberization and waxes where the ants rear their brood, and highly absorptive warty-walled chambers in which the ants defecate to fertilize the plant [11**,70]. Transcriptomic analyses of the different types of chambers reveal that warts inside domatium cavities may functionally be analogous to roots [73*]. This is supported by the upregulation of genes related to auxin metabolism, transport, and response as well as key root developmental genes – such as *FEZ*, which participate in the control of the cell division plane in root stem cells [74]. Warty-walled cavities show up-regulation of nitrogen uptake genes (e.g. *Ammonium Transporter 1;1* and *1;2*) that take up ant-derived nutrients, and 54 stress response genes (including *SSL4*, which is involved in response against fungal pathogens [75], or pectin methylesterase 17, which responds to gram-negative bacteria [76], which may play a role protection of this permeable tissue from pathogens. Wax (*KCS6* and *MYB94/96*) and suberin (*ABC6 & 20*) biosynthesis genes are up-regulated in smooth-walls [73*].

Conclusions and outlook

The morphological, phylogenetic, and developmental diversity of domatia across plants suggests that domatia development integrates multiple genetic pathways across systems. Stem domatia appear to often involve several developmental processes, with cell death playing an important role, likely often with differential growth and sometimes cell separation and ant-mediated tissue destruction. The latter is always controlled by a weakening (e.g. prostoma, Box 1) or layers of cells with oxalate crystals which delineate what tissue can be excavated [32*]. By contrast, leaf domatia appear to rely extensively on regional differences in growth leading to deformation, likely often with initial cell separation. A divergent type appears to be mite tuft domatia, which rely more heavily on the regulation of trichome regulators. While differences exist across domatia types, the relative importance of different developmental processes and whether they rely on the same developmental genetic pathways across distinct taxa is an open question.

While relatively little is known about the developmental genetics of domatia, anatomical studies have sketched the outlines of morphogenesis of some of domatia diversity, hinting at co-option of conserved developmental mechanisms and suggesting multiple testable hypotheses. For both ant and mite domatia, development may stem from the co-option of conserved developmental genetic pathways involved in plant organ formation, such as genes leaf polarity, or genes involved in trichome development. However, homoplastic traits often blend convergent and novel genes and regulators, and further detailed developmental and genetic characterisation is required to test these hypotheses. Key experiments needed include detailed morphological characterisation of domatia development and genetic analysis to determine co-option or divergence of conserved developmental regulators.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is provided in Supplementary Materials

Acknowledgements

GC is supported by a NERC Independent Research Fellowship NE/S014470/3 and an ERC/UKRI frontier research grant (EP/X026868/1). JPE gratefully acknowledges support from BBSRC grants BB/V008129/1 and BB/X000559/1. E.J.R is partially funded by US National Science Foundation grant DEB-1831164. M.G.W. is funded by US National Science Foundation grants DEB-1831164 and DEB-2236747. We thank Beatriz Goncalves and one anonymous reviewer for critical comments that helped improve our manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pbi.2024.102647.

References

Papers of particular interest, published within the period of review, have been highlighted as:

* of special interest
** of outstanding interest

1. Weber MG, Keeler KH: **The phylogenetic distribution of extrafloral nectaries in plants**. *Ann Bot* 2013, **111**:1251–1261.

2. Chomicki G, Renner SS: **Phylogenetics and molecular clocks reveal the repeated evolution of ant-plants after the late Miocene in Africa and the early Miocene in Australasia and the Neotropics**. *New Phytol* 2015, **207**:411–424.

3. Myers A, Martin B, Yonenaga J, Agrawal AA, Weber MG: **A global assessment of plant-mite mutualism and its ecological drivers**. *bioRxiv*. https://doi.org/10.1101/2024.09.24.614831.

4. O'Dowd DJ, Willson MF: **Associations between mites and leaf domatia**. *Trends Ecol Evol* 1991, **6**:179–182.

5. * Maccracken SA, Miller IM, Labandeira CC: **Late Cretaceous domatia reveal the antiquity of plant–mite mutualisms in flowering plants**. *Biol Lett* 2019, **15**, 20190657.

This study reports the oldest fossil know of a (pit) domatia, dating to 75 million years in Utah, extending the mite domatia fossil record by 25 million years to the Late Cretaceous.

6. Chanam J, Borges RM: **Cauline domatia of the ant-plant *Humboldtia brunonis* (Fabaceae)**. *Flora* 2017, **236**:58–66.

7. Gutiérrez-Valencia J, Chomicki G, Renner SS: **Recurrent breakdowns of mutualisms with ants in the neotropical ant-plant genus *Cecropia* (Urticaceae)**. *Mol Phylogenet Evol* 2017, **111**:196–205.

8. Chomicki G, Ward PS, Renner SS: **Macroevolutionary assembly of ant/plant symbioses: *pseudomyrmex* ants and their ant-housing plants in the Neotropics**. *Proc R Soc A B* 2015, **282**, 20152200.

9. Chomicki G, Renner SS: **Partner abundance controls mutualism stability and the pace of morphological change over geologic time**. *Proc Natl Acad Sci USA* 2017, **114**:3951–3956.

10. Chomicki G, Renner SS: **Obligate plant farming by a specialized ant**. *Nat Plants* 2016, **2**:1–4.

11. ** Chomicki G, Renner SS: **Farming by ants remodels nutrient uptake in epiphytes**. *New Phytol* 2019, **223**:2011–2023.

Using year-long field experiments, isotope labelling, Computed-tomography scanning and evolutionary analyses, this paper demonstrate that the evolution of obligate plant farming by ants completely remodelled plant nutrition. Domatia of ant-farmed plants evolved hyper-absortive warts that function as root hairs. The ants defecate on warts, which provides over 40% of the total nitrogen to the plant.

12. * Sarath E, Ezaki K, Sasaki T, Maekawa Y, Sawada Y, Hirai MY, Soejima A, Tsukaya H: **Morphological characterization of domatium development in *Callicarpa saccata***. *Ann Bot* 2020, **125**:521–532.

This anatomical paper dissects the development of leaf pouch domatia in *Callicarpa saccata*, testing for the 'curling leaf' vs. 'warping' hypotheses. It shows that the domatia follows the warping scenario, wherein cell proliferation at the blade/petiole junction at the base of the leaf generates domatium tissue (rather than marginal growth leading the leaf end to roll on itself as in the former hypothesis).

13. * Leroy C, Jauneau A, Quilichini A, Dejean A, Orivel J: **Comparative structure and ontogeny of the foliar domatia in three neotropical myrmecophytes**. *Am J Bot* 2010, **97**:557–565.

This paper compare leaf pouch domatia development in three ant-plants, identifying that in Hirtella, the domatia has an intermediate form – consistent with its different developmental origin. It also identifies that in all species, leaf domatium tissue lacks the standard leaf anatomical differentiation in mesophyll and palisade parenchyma, suggesting a cost.

14. Bonato V, Cogni R, Venticinque EM: **Ants nesting on *Cecropia purpurascens* (Cecropiaceae) in central Amazonia: influence of tree height, domatia volume and food bodies**. *Sociobiology* 2003, **42**:719–772.

15. Fiala B, Maschwitz U: **Domatia as most important adaptations in the evolution of myrmecophytes in the paleotropical tree genus *Macaranga* (Euphorbiaceae)**. *Plant Syst Evol* 1992, **180**:53–64.

16. * Brouat C, McKey D: **Origin of caulinary ant domatia and timing of their onset in plant ontogeny: evolution of a key trait in horizontally transmitted ant-plant symbioses**. *Biol J Linn Soc* 2000, **71**:801–819.

This is the first study to show that stem domatia breaks down the leaf/stem allometry rule known as 'Corner's rule', imposing a cost to the domatia and implying that a minimum stem diameter is required for domatia to evolve.

17. Brouat C, McKey D: **Leaf-stem allometry, hollow stems, and the evolution of caulinary domatia in myrmecophytes**. *New Phytol* 2001, **151**:391–406.

18. Chomicki G, Renner SS: **Climate and symbioses with ants modulate leaf/stem scaling in epiphytes**. *Sci Rep* 2019, **9**:2624.

19. Burin G, Campbell LC, Renner SS, Kiers ET, Chomicki G: **Mutualisms drive plant trait evolution beyond interaction-related traits**. *Ecol Lett* 2024, **27**, e14379.

20. ** Leichty AR, Poethig RS: **Development and evolution of age-dependent defences in ant-acacias**. *Proc Natl Acad Sci USA* 2019, **116**:15596–15601.

This paper demonstrates that timing of development of domatia, as well as food rewards (extrafloral nectaries and protein-rich beltian bodies) in the ant-acacias rely in the miR156/157 pathway and their SPL targets. Domatia develops following a predictable decline in miR156/157 and associated increase in their SPL targets, suggesting that their onset occurred by co-option of a conserved developmental timing pathway.

21. He J, Xu M, Willmann MR, McCormick K, Hu T, Yang L, Starker CG, Voytas DF, Meyers BC, Poethig RS: **Threshold-dependent repression of SPL gene expression by miR156/miR157 controls vegetative phase change in *Arabidopsis thaliana***. *PLoS Genet* 2018, **14**, e1007337.

22. Nishida S, Tsukaya H, Nagamasu H, Nozaki M: **A comparative study on the anatomy and development of different shapes of domatia in *Cinnamomum camphora* (Lauraceae)**. *Ann Bot* 2006, **97**:601–610.

23. Ward PS: **Phylogenetic analysis of pseudomyrmecine ants associated with domatia-bearing plants**. In *Ant-plant interactions*. Edited by Huxley CR, Cutler DF, Oxford: Oxford University Press; 1991:335–352.

24. Larsen A, Philpott SM: **Twig-nesting ants: the hidden predators of the coffee berry borer in Chiapas, Mexico**. *Biotropica* 2010, **42**:342–347.

25. * Blüthgen N, Wesenberg J: **Ants induce domatia in a rain forest tree (*Vochysia vismiaefolia*)**. *Biotropica* 2001, **33**:637–642.

This paper reports the first and only known (stem) domatia that is inducible by ants. This suggests that an early evolutionary stage for domatia formation involves wound-induced pathways activated by ants piercing through the stem tissue to nest in the pith.

26. Creelman RA, Mullet JE: **Biosynthesis and action of jasmonates in plants**. *Annu Rev Plant Biol* 1997, **48**:355–381.

27. O'donnell PJ, Calvert C, Atzorn R, Wasternack C, Leyser HMO, Bowles DJ: **Ethylene as a signal mediating the wound response of tomato plants**. *Science* 1996, **274**:1914–1917.

28. Love J, Björklund S, Vahala J, Hertzberg M, Kangasjärvi J, Sundberg B: **Ethylene is an endogenous stimulator of cell division in the cambial meristem of *Populus***. *Proc Natl Acad Sci USA* 2009, **106**:5984–5989.

29. Sehr EM, Agusti J, Lehner R, Farmer EE, Schwarz M, Greb T: **Analysis of secondary growth in the *Arabidopsis* shoot reveals a positive role of jasmonate signalling in cambium formation**. *Plant J* 2010, **63**:811–822.

30. Etchells JP, Provost CM, Turner SR: **Plant vascular cell division is maintained by an interaction between PXY and ethylene signalling**. *PLoS Genet* 2012, **8**, e1002997.

31. Fiala B, Grunsky H, Maschwitz U, Linsenmair KE: **Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association**. *Oecologia* 1994, **97**:186–192.

32. * Tepe EJ, Kelley WA, Rodriguez-Castañeda G, Dyer LA, Miller J: **Characterizing the cauline domatia of two newly discovered Ecuadorian ant plants in *Piper*: an example of convergent evolution**. *J Insect Sci* 2009, **9**:27.

This anatomical paper identify two different mechanisms for stem domatia development in Piper. In the section Macrostachys, domatia develops by large, loose pith cells that are easily excavated and then become lined with a suberised tissue that produce food rewards for its obligate ant mutualist. In *P. immutatum* and *P. pterocladum*, the domatia develops by lysogyny and there is no lining tissue.

33. Tepe EJ, Vincent MA, Watson LE: **Stem diversity, cauline domatia, and the evolution of ant–plant associations in Piper sect. Macrostachys (Piperaceae)**. *Am J Bot* 2007, **94**:1–11.

34. Wunderling A, Ripper D, Barra-Jimenez A, Mahn S, Sajak K, Targem MB, Ragni L: **A molecular framework to study periderm formation in *Arabidopsis***. *New Phytol* 2018, **219**: 216–229.

35. Xiao W, Molina D, Wunderling A, Ripper D, Vermeer JE, Ragni L: **Pluripotent pericycle cells trigger different growth outputs by integrating developmental cues into distinct regulatory modules**. *Curr Biol* 2020, **30**:4384–4398.

36. Stace C: **Cuticular studies as an aid to plant taxonomy**. *Bull Brit Mus (Nat Hist) Bot* 1965, **4**:3–78.

37. Leroy C, Jauneau A, Quilichini A, Dejean A, Orivel J: **Comparison between the anatomical and morphological structure of leaf blades and foliar domatia in the ant-plant *Hirtella physophora* (Chrysobalanaceae)**. *Ann Bot* 2008, **101**:501–507.

38. Sarath EE: *Morphological and molecular characterisation of domatium development in myrmecophytes*. University of Tokyo; 2019. Doctoral dissertation.

39. Ngoc Anh Tô: **Sur la structure anatomique et l'ontogénèse des acarodomaties et les interprétations morphologiques qui paraissent s'en dégager**. *Adansonia* 1966, **6**:147–151.

40. Schnell R, Cusset G, Tchinaye V, Anh Tô Ngoc: **Contribution à l'étude des 'acarodomaties' la question des aisselles de nervures**. *Revue Gén Bot* 1968, **75**:5–64.

41. O'Dowd DJ, Willson MF: **Leaf domatia and mites on Australasian plants: ecological and evolutionary implications**. *Biol J Linn Soc* 1989, **37**:191–236.

42. * * Whitewoods CD, Gonçalves B, Cheng J, Cui M, Kennaway R, Lee K, Bushell C, Yu M, Piao C, Coen E: **Evolution of carnivorous traps from planar leaves through simple shifts in gene expression**. *Science* 2020, **367**:91–96.

This paper shows that restriction of the adaxial leaf domain is responsible for the cup-shaped growth resulting in a trap in the carnivorous plant *Utricularia gibba*. Similar morphologies occur in leaf domatia, suggesting that a similar mechanism could be involved in generating leaf pouch domatia.

43. Rebocho AB, Southam P, Kennaway JR, Bangham JA, Coen E: **Generation of shape complexity through tissue conflict resolution**. *Elife* 2017, **6**, e20156.

44. Ha CM, Kim GT, Kim BC, Jun JH, Soh MS, Ueno Y, Machida Y, Tsukaya H, Nam HG: **The *BLADE-ON-PETIOLE 1* gene controls leaf pattern formation through the modulation of meristematic activity in *Arabidopsis***. *Development* 2003, **130**:161–172.

45. Jun JH, Ha CM, Fletcher JC: ***BLADE-ON-PETIOLE1* coordinates organ determinacy and axial polarity in Arabidopsis by directly activating ASYMMETRIC LEAVES2**. *Plant Cell* 2010, **22**:62–76.

46. Norberg M, Mattias H, Nilsson O: **The BLADE ON PETIOLE genes act redundantly to control the growth and development of lateral organs**. *Development* 2005:2203–2213.

47. Ha CM, Jun JH, Nam HG, Fletcher JC: **BLADE-ON-PETIOLE1 and 2 control Arabidopsis lateral organ fate through regulation of LOB domain and adaxial-abaxial polarity genes**. *Plant Cell* 2007, **19**:1809–1825.

48. Golz JF, Keck EJ, Hudson A: **Spontaneous mutations in KNOX genes give rise to a novel floral structure in *Antirrhinum***. *Curr Biol* 2002, **12**:515–522.

49. Khan M, Xu M, Murmu J, Tabb P, Liu Y, Storey K, McKim SM, Douglas CJ, Hepworth SR: **Antagonistic interaction of BLADE-ON-PETIOLE1 and 2 with BREVIPEDICELLUS and PENNYWISE regulates Arabidopsis inflorescence architecture**. *Plant Physiol* 2012, **158**:946–960.

50. Belles-Boix E, Hamant O, Witiak SM, Morin H, Traas J, Pautot V: **KNAT6: an *Arabidopsis* homeobox gene involved in meristem activity and organ separation**. *Plant Cell* 2006, **18**: 1900–1907.

51. Husbands AY, Benkovics AH, Nogueira FT, Lodha M, Timmermans MC: **The ASYMMETRIC LEAVES complex employs multiple modes of regulation to affect adaxial-abaxial patterning and leaf complexity**. *Plant Cell* 2015, **27**: 3321–3335.

52. Nikovics K, Blein T, Peaucelle A, Ishida T, Morin H, Aida M, Laufs P: **The balance between the MIR164A and CUC2 genes controls leaf margin serration in Arabidopsis**. *Plant Cell* 2006, **18**:2929–2945.

53. Hasson A, Plessis A, Blein T, Adroher B, Grigg S, Tsiantis M, Boudaoud A, Damerval C, Laufs P: **Evolution and diverse roles of the CUP-SHAPED COTYLEDON genes in Arabidopsis leaf development**. *Plant Cell* 2011, **23**:54–68.

54. Serra L, Perrot-Rechenmann C: **Spatiotemporal control of cell growth by CUC3 shapes leaf margins**. *Development* 2020, **147**: dev183277.

55. Nath U, Crawford BC, Carpenter R, Coen E: **Genetic control of surface curvature**. *Science* 2003, **299**:1404–1407.

56. Koyama T, Mitsuda N, Seki M, Shinozaki K, Ohme-Takagi M: **TCP transcription factors regulate the activities of ASYMMETRIC LEAVES1 and miR164, as well as the auxin response, during differentiation of leaves in Arabidopsis**. *Plant Cell* 2010, **22**:3574–3588.

57. Tanaka Y, Yamamura T, Oshima Y, Mitsuda N, Koyama T, Ohme-Takagi M, Terakawa T: **Creating ruffled flower petals in *Cyclamen persicum* by expression of the chimeric cyclamen TCP repressor**. *Plant Biotechnol* 2011, **28**:141–147. 2011.

58. Koyama T, Mitsuda N, Seki M, Shinozaki K, Ohme-Takagi M: **TCP transcription factors regulate the activities of ASYMMETRIC LEAVES1 and miR164, as well as the auxin response, during differentiation of leaves in Arabidopsis**. *Plant Cell* 2010, **22**:3574–3588.

59. Michelangeli FA: **Tococa (Melastomataceae)**. *Flora Neotrop* 2005:1–114.

60. Izzo TJ, Vasconcelos HL: **Cheating the cheater: domatia loss minimizes the effects of ant castration in an Amazonian ant-plant**. *Oecologia* 2002, **133**:200–205.

61. Chomicki G, Bidel LP, Baker WJ, Jay-Allemand C: **Palm snorkelling: leaf bases as aeration structures in the mangrove palm (*Nypa fruticans*)**. *Bot J Linn Soc* 2014, **174**:257–270.

62. Taylor JE, Whitelaw CA: **Signals in abscission**. *New Phytol* 2001, **151**:323–340.

63. Olsson V, Butenko MA: **Abscission in plants**. *Curr Biol* 2018, **28**:R338–R339.

64. Stenvik GE, Tandstad NM, Guo Y, Shi CL, Kristiansen W, Holmgren A, Clark SE, Aalen RB, Butenko MA: **The EPIP peptide of INFLORESCENCE DEFICIENT IN ABSCISSION is sufficient to induce abscission in Arabidopsis through the receptor-like kinases HAESA and HAESA-LIKE2**. *Plant Cell* 2008, **20**:1805–1817.

65. Shi CL, Stenvik GE, Vie AK, Bones AM, Pautot V, Proveniers M, Aalen RB, Butenko MA: **Arabidopsis class I KNOTTED-like homeobox proteins act downstream in the IDA-HAE/HSL2 floral abscission signaling pathway**. *Plant Cell* 2011, **23**:2553–2567.

66. Merklinger FF, Baker WJ, Rudall PJ: **Comparative development of the rattan ocrea, a structural innovation that facilitates ant–plant mutualism**. *Plant Syst Evol* 2014, **300**:1973–1983.

67. Jouannic S, Collin M, Vidal B, Verdeil JL, Tregear JW: **A class I KNOX gene from the palm species *Elaeis guineensis* (Arecaceae) is associated with meristem function and a distinct mode of leaf dissection**. *New Phytol* 2007, **174**:551–568.

68. Nowak JS, Bolduc N, Dengler NG, Posluszny U: **Compound leaf development in the palm *Chamaedorea elegans* is KNOX-independent**. *Am J Bot* 2011, **98**:1575–1582.

69. Jebb MHP: **Cavity structure and function in the tuberous Rubiaceae**. In *Ant-plant interactions*. Edited by Huxley CR, Cutler DE; 1991:374–390. 1991.

70. Huxley CR: **The ant-plants *Myrmecodia* and *Hydnophytum* (Rubiaceae), and the relationships between their morphology, ant occupants, physiology and ecology**. *New Phytol* 1978, **80**:231–268.

71. Tsukaya H, Ohtake Y: **Cavity and entrance pore development in ant plant hypocotyls**. *Front Plant Sci* 2023, **14**, 1234650.

72. Chomicki G, Kadereit G, Renner SS, Kiers ET: **Tradeoffs in the evolution of plant farming by ants**. *Proc Natl Acad Sci USA* 2020, **117**:2535–2543.

73. * Pu Y, Naikatini A, Pérez-Escobar OA, Silber M, Renner SS, Chomicki G: **Genome-wide transcriptome signatures of ant-farmed *Squamellaria* epiphytes reveal key functions in a unique symbiosis**. *Ecol Evol* 2021, **11**:15882–15895.

First transcriptomic analysis of hypocotyl domatia, focusing on the differentiation of the distinct inner domatium tissue types. It identified a number of interesting candidate genes associated with the function of the warty vs. smooth cavity walls, the former present functional and developmental signatures of adventitious roots.

74. Willemsen V, Bauch M, Bennett T, Campilho A, Wolkenfelt H, Xu J, Haseloff J, Scheres B: **The NAC domain transcription factors FEZ and SOMBRERO control the orientation of cell division plane in Arabidopsis root stem cells**. *Dev Cell* 2008, **15**:913–922.

75. Sohani MM, Schenk PM, Schultz CJ, Schmidt O: **Phylogenetic and transcriptional analysis of a strictosidine synthase-like gene family in *Arabidopsis thaliana* reveals involvement in plant defence responses**. *Plant Biol* 2009, **11**:105–117.

76. Bethke G, Grundman RE, Sreekanta S, Truman W, Katagiri F, Glazebrook J: **Arabidopsis PECTIN METHYLESTERASEs contribute to immunity against *Pseudomonas syringae***. *Plant Physiol* 2014, **164**:1093–1107.

77. * Barba P, Loughner R, Wentworth K, Nyrop JP, Loeb GM, Reisch BI: **A QTL associated with leaf trichome traits has a major influence on the abundance of the predatory mite Typhlodromus pyri in a hybrid grapevine population**. *Horticult Res* 2019, **6**:87.

First QTL analysis for mite tuft domatia in grapewine. It idenfied several gene candidates associated with mite domatia, notably several genes involved in trichome development.

78. * LaPlante ER, Fleming MB, Migicovsky Z, Weber MG: **Genome-wide association study reveals a genomic region associated with mite-recruitment phenotypes in the domesticated grapevine (*Vitis vinifera*)**. *Genes* 2021, **12**:1013.

First GWAS analysis for mite tuft domatia in grapewine. It identified several interesting candidates associated with mite domatia, and their size and density, specifically genes involved in trichome development, leaf development, and defence against fungal pathogens.

79. Zhang Y, Schwarz S, Saedler H, Huijser P: **SPL8, a local regulator in a subset of gibberellin-mediated developmental processes in Arabidopsis**. *Plant Mol Biol* 2007, **63**:429–439.

80. Han G, Li Y, Yang Z, Wang C, Zhang Y, Wang B: **Molecular mechanisms of plant trichome development**. *Front Plant Sci* 2022, **13**, 910228.

81. Behringer C, Bastakis E, Ranftl QL, Mayer K, Schwechheimer C: **Functional diversification within the family of B-GATA transcription factors through the leucine-leucine-methionine domain**. *Plant Physiol* 2014, **166**:293–305.

82. Chitwood DH, Ranjan A, Martinez CC, Headland LR, Thiem T, Kumar R, Covington MF, Hatcher T, Naylor DT, Zimmerman S, Downs N: **A modern ampelography: a genetic basis for leaf shape and venation patterning in grape**. *Plant Physiol* 2014, **164**:259–272.

83. Norton AP, English-Loeb G, Gadoury D, Seem RC: **Mycophagous mites and foliar pathogens: leaf domatia mediate tritrophic interactions in grapes**. *Ecology* 2000, **81**:490–499.

84. Janzen DH: **Coevolution of mutualism between ants and Acacias in central America**. *Evolution* 1966, **20**:249–275.

85. Heil M, McKey D: **Protective ant-plant interactions as model systems in ecological and evolutionary research**. *Annu Rev Ecol Evol Syst* 2003, **34**:425–553.

86. Koricheva J, Nykänen H, Gianoli E: **Meta-analysis of trade-offs among plant antiherbivore defences: are plants jacks-of-all-trades, masters of all?** *Am Nat* 2004, **163**:E64–E75.

87. Ballhorn DJ, Kautz S, Lion U, Heil M: **Trade-offs between direct and indirect defences of lima bean (*Phaseolus lunatus*)**. *J Ecol* 2008, **96**:971–980.

88. Graham CD, Forrestel EJ, Schilmiller AL, Zemenick AT, Weber MG: **Evolutionary signatures of a trade-off in direct and indirect defences across the wild grape genus**. *Vitis. Evolution* 2023, **77**:2301–2313.

89. Ramírez-Barahona S, Sauquet H, Magallón S: **The delayed and geographically heterogeneous diversification of flowering plant families**. *Nat Ecol Evol* 2020, **4**:1232–1238.

90. Yu G, Smith DK, Zhu H, Guan Y, Lam TT-Y: **ggtree: an r package for visualization and annotation of phylogenetic trees with their covariates and other associated data**. *Methods Ecol Evol* 2017, **8**:28–36.

91. R Core Team: *R: a language and environment for statistical computing*. R Foundation for Statistical Computing; 2024.