
In this taxonomic paper Almeda is the first (to my knowledge) to find and report a relationship between a melastome, *Clidemia hammelii*, and a mite inhabiting its domatia. The genus of mite is *Ololaelaps* (Gamasida, familia Laelapidae) and G. W. Krantz (cited in Almeda, 1989) stated that this was an unusual habitat for this genus of mites because they are usually found on moss or leaf litter, or in nests of small mammals.


A significant positive relationship between size of domatia and abundance naturally occurring predatory mites was found. Mites also spent more time and deposited more eggs on leaves with unblocked domatia. Because the domatia in *Vitis riparia* are so small the results indicate that the presence of domatia is important and not just access to leaf veins. Elevated predatory mite abundance in response to domatia however did not translate into decreases in abundance of a pest mite. The authors recommend breeding for well developed domatia in grape plants.


Jacobs explains the origin of the word in greek which means bedroom but in biological terms it is a diminutive for house. This extensive paper that domatia are: a) bound to nerve axils, b) in leaf undersides and c) occur in woody dicots. He recognized four main kinds of domatia that may also be combined in a single domatium: 1) a pit in the leaf surface, 2) a pocket of tissue in a nerve axil, 3) a tuft of hairs or 4) a dome with an opening at its top. No taxonomic utility for domatia was found and they might be present only in certain parts of the life stage. Differentiating domatia from glands may be difficult with dry specimens. The author did some experiments and suggests that absence of the mites does not affect normal development of the domatia. Although on the one side the damaging effect of animals on domatia in aging leaves may be considerable, it has not been well studied and domatia might on the other hand increase the liability of nerve axils to actions on the part of gall mites. Jacobs states: “the biological relationship between domatia-bearing plants and Acari has never been proven and the idea can be traced to suppositions concerning myrmecophily, which are obsolete since a long time. He goes further to say there are indications
that all questions for the use of domatia have their first origin in a non biological field of human interest.


The genus Tococa has 47 recognized species, 30 of which have ant domatia (formicaria). Exclusion experiments with three species of Tococa occupying different environments demonstrated the role of ants as defense against herbivores. Herbivory rates were higher in open and disturbed areas than in forest understory. Ant exclusion experiments showed both aggressive and timid ants protect their host plants fighting leaf cutting ants off of the plants as well as removing eggs of Lepidoptera and Coleoptera.


This first species of obligatory domatia inhabiting thrips undergoes all life stages within the domatia of Psychotria gracilliflora and is described in the well named genus Domatiathrips from a lowland rainforest in Costa Rica. Mounds finds no obvious benefit for the plant, nevertheless he did no experiments or longtime obervations and coincides with Jacobs (1966) in that no obvious mutualistic relationship is evident or has been proven between mites and leaf domatia.


In separate experiments the authors examined whether domatia in the wild grape Vitis riparia provide protection against drying humidity conditions or predaceous arthropods to two species of beneficial mites. For both taxa of beneficial mite the domatia significantly increased mite survivorship against predatory arthropods but there was no evidence for any protection against humidity suggesting a main function for domatia of protection for the mites against predatory arthropods.


In this paper the authors examine the influence of domatia on the abundance of the tydeid mite Orthotydeus lambi on the riverbank grape Vitis riparia and its impact on a key fungal pathogen, the grape powdery mildew, Uncinula necator. In field experiments the authors either blocked domatia or used plant clones with
different sized domatia. Mites were more abundant both in plants with unblocked domatia and in plants with larger domatia. In both treatment the mites reduced the mildew from the plants.


Although circumstancial evidence suggesting a mutualistic mite-plant relationship is strong, O'Dowd & Willson feel the necessary experiments remain to be done. For the rest, this paper is mostly a summary of the next one. Additional interesting observations include the citation of another paper finding domatia to decline in frequency with increasing aridity, rare in most dry forests and woodlands.


Interesting initial overview of the inconcordance of opinion about the significance of domatia. They examined 37 plant species in Australasia by collecting leaf samples from several sites. The leaves were collected from different individuals, several shoots per individual and several leaves per shoot to be able to determine which levels (individual, shoot or leaf) explain most of the variation in either domatia number per leaf or mite association using nested ANOVA. They also did a rigorous description of domatia considering morphology, number and anatomy. Verification of a mite association was corroborated evidence of the presence of mites in any of their life stage or presence of faeces. Mites were categorized in three roles: predaceous, saprophagous-fungivorous and herbivorous. A detailed account of why they classified the mites this way is given. Detailed descriptions of the domatia are also given and anatomical work showed that the domatia do not have specialized structures for trapping and digesting insects. Interestingly eriophyd mites were found in some leaves and these mites are known to cause abnormal development of plant tissues. Also noted is that although mite domatia differed considerably in their anatomical makeup, their size was very constant. Foliar domatia are known from the fossil record from the mid-Eocene, and nowadays domatia-bearing plants may constitute for example up to 15% of the total tree diversity of forests north of Queensland and 31% in New Zealand.

The average number and density of domatia per leaf varied enormously and ranged from less than 1 to 27. No evident association occurred between domatia abundance per leaf and plant growth form, type of domatium, or provenance. Average number of primary veins per leaf and leaf area were equally good predictors of domatia number per leaf. In New Zealand 58% of the species in the genus Coprosma have domatia (31/53) but also hear they are very variable and narrower leaves usually lack domatia
Arthropods were commonly encountered inside domatia examined and around 85% of them were mites. Predaceous and fungivorous/saprophagous mites dominated domatia associations in 21 out of the 24 families in which frequency of mites was quantified. Evidence of occupation by mites ranged from 6% to 92% with a median of 51% resulting in the presence of mites in more than half of the sample of more than 24000 domatia. Evidence of mites differed significantly between regions being very common in New Zealand, Victoria and Queensland and significantly less common in New Guinea. Most of the variation in within species mite occupancy of domatia lay on the leaves suggesting that patterns of association are probably at the leaf or domatia level. Leaf phenology and development stage is shown to be significant for finding mites, older leaves being occupied by more mites suggesting that mite populations build up year by year. Older leaves also had more mite diversity. Interestingly older leaves had more oribatid mites, “coincident with a higher average epiphyll cover on older leaves; epiphylls probably probably provide the main food resource for these mites.”

The biological significance of domatia is discussed through four possibilities:
A) Non-functional explanations. 1) The spandrels of San Marco. Attempts to explain presence of domatia because of morphological and phylogenetic processes and constraints. This argument is not very strong for domatia are lacking in species with major veins and present in some taxa without them. It is suggested that a leaf vein may be the way for a leaf to make a domatium. 2) Chance association of animals with domatia. The authors argue that chance alone cannot explain the high frequency of occupancy of domatia in the species in their survey. They also cite several studies that frequently found mites within domatia.
B) Functional interpretations not involving mites. 1) Physiological function. Although several authors have considered that domatia might function in gas or water exchange there is no evidence to support this. 2) Insect traps. Presence of all life stages within domatia as well as free mite activity from the domatia excludes this possibility. 3) Bacterial symbionts. A study found no specialized anatomical structures characteristic of all of the well-developed bacterial-plant symbionts negating this hypothesis.
C) Antagonistic interactions with mites. 1) Domatia are galls induced by mites. Galls and domatia are differentiable by looking at cell structure. Fixation of domatia at the species level further argues against this. There is general agreement mites do not result from irritation or induction by mites. 2) Protection of leaves from damage by mites. No evidence for this suggestion which states that the domatal hairs in the Dipterocarpaceae might protect the leaves from the mites. 3) Localization of mite damage. This comes from looking at lizards with mite pockets that have been hypothesized to have evolved the pockets to localize might damage. No consistent damage within domatia as well as lack of predominance of phytophagous mites within them suggests this to be unlikely.
D) Mutualistic relationships with mites. 1) Nutritional hypothesis. States that domatia help break up mite refuse. Although there is no experimental dat, it
seems highly unlikely. 2) **Protection hypothesis.** It has been shown that herbivores and fungi which can be pathogenic affect plant survivorship, growth and reproduction. Lundstroem found mite spores in the mites faeces. The authors also showed that most domatia inhabiting mites are fungivorous so domatia are likely to be advantageous. Beside the sheltering for reproduction and development, domatia might also provide a microclimate that protects poorly cutinized mites. Some mites that are also present in domatia have been documented as biological control agents which further supports their possible importance for plants.

Differences between ant domatia and might domatia associations include size of the domatia, higher cost in ant domatia mutualisms especially if they involve extra-floral nectar and lack of sociality in might which might prevent a more specialized relationship like that of ant plants from evolving. Occurence of both on the same plant is rare.


Examination of the domatia of 32 plant species from California, Hawaii and Costa Rica showed that 31 of the 32 (97%) contained mites. Mites were found in 48% of the sampled leaves. 26 of the 31 species contained mites considered to be beneficial while 6 of the 31 had mites considered to be harmful. The authors hypothesize a widespread mutualism between plants with domatia and beneficial mites: leaf domatia serve as shelters and nurseries for mites which in turn eat phytophagous arthropods and pathogens using the plants.


This experiment was carried out in south-east Brazil. It is informative among other things because little is known of domatia in the tropics, less so than in temperate regions. They used saplings of *Cupania vernalis* to examine the effect of domatia on: 1) mites and other arthropods and 2) damage caused by fungi and herbivorous arthropods. The amount of predaceous mites in plants with open domatia was higher than in plants with blocked domatia; the amount of fungivorous and phytophagous mites stayed the same. Plants in which the domatia were blocked had increased chlorosis apparently from higher attacks from eriophyd mites.

Mite domatia were found to be occupied 66% of the time by mites in different parts of their life cycle. On average 70% of the mites found on leaves were found in the domatia and over three quarters of these were found to be potentially beneficial to the plant. When species were pooled across sites, leaves of domatia-bearing plants had significantly more predaceous mites than those of plants without domatia. The author states her results are concordant with other that suggest a mutualistic association.