

Mite-plant mutualism:

leaf domatia of African plants house beneficial mites.

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A fungivorous oribatid mite inside a domatium of *Chionanthus foveolatus*.

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Abstract

Leaf domatia, specialized chambers or hair tufts in the vein axils on the underside of leaves, are present in many woody angiosperm species. Recent surveys on four continents have shown that mites are commonly associated with leaf domatia. This study extends the list to include the African continent. Mites in all life history stages, including eggs, were found to be common in the domatia of two forest trees, *Ocotea bullata* (0.62 mites per domatium) and *Chionanthus foveolatus* (1.95). Like on other continents, the mites in the domatia of these two species belong primarily to predatory and fungivorous taxa. Of the hypotheses offered to explain these associations, protective mutualism has received the most attention. However, only circumstantial evidence has been presented in support of a mutually beneficial relationship. I found that the leaves of *C. foveolatus* support much larger mite populations than the domatium-less leaves of a sympatric species, *Olea capensis macrocarpa* ("species" explains 44% of variation in mite numbers in a nested ANOVA). Similarly, for both species mites are much more common in domatia than in domatium-less vein axils on the same leaf. These result suggests that domatia enhance mite fitness, probably by providing a humid, protected refuge on the otherwise barren leaf surface. It has been suggested that mites, in return, protect domatium-bearing plants by feeding on epiphylls and microherbivores. I found that *O. bullata* leaves with more predatory mites in the domatia suffer less herbivory damage ($r = 0.18$, slope = -0.66, $df = 99$, $p < 0.05$). This result is confirmed in an experimental study; leaves with blocked domatia suffer significantly more herbivory damage than control leaves after a period of 18 months ($F = 11.8$, $d.f. = 19$, $P < 0.0006$). Mite exclusion treatments did however not have an effect on the abundance of fungi on the leaves of *O. bullata* ("treatment" accounts for 0% of the variation in a nested ANOVA); nor was there any relationship between the abundance of fungivorous oribatid mites in the domatia of *C. foveolatus* and the abundance of a sooty leaf fungus ($R^2 = 0.46\%$, $d.f. = 47$). Leaf age is identified as a very important variable in phylloplane ecology.

Introduction

Mite-domatium associations: old viewpoints and new evidence

Animal mediated pollination and dispersal are the most familiar, and well studied examples of animal-plant mutualism. During pollination and dispersal, the interaction between plant and animal is a brief one. Long-term mutualistic associations between plants and animals have, until recently, been thought to be restricted to a few cases of ant-plant mutualism (Beattie 1985).

In 1887 Axel Lundstroem first proposed that leaf domatia, specialized chambers or hair tufts in the vein axils on the underside of leaves, house predatory and fungivorous mites that devour plant enemies. The idea has met with considerable resistance from scientist ever since (Hamilton 1897; Jacobs 1966). However, in the last three years there has been a renewed interest the association between leaf domatia and leaf-dwelling mites (O'Dowd and Willson 1989, 1991). These recent studies have given a quantitative basis for the evaluation of Lundstroem's hypothesis of mutualism.

Surveys conducted in North and Central America (Pemberton and Turner 1989; Willson 1991), Australia, New Zealand and Papua New Guinea (O'Dowd and Willson 1989) have shown that mites are commonly associated with domatia and comprise over 90% of the domatal fauna. On plants that have domatia, the concentration of mites is almost always higher in domatia than in vein axils lacking domatia or on the leaf blade (O'Dowd and Willson 1989). On leaves without domatia, the numbers of mites are much lower than on leaves with domatia (Walter and O'Dowd 1992a). This is true within plant species, between congeners, and across unrelated species.

Removal of the axillary hair tufts of *Viburnum tinus* significantly reduced the total number of mites per leaf (Walter and O'Dowd 1992a). Similarly, when leaf domatia of a rainforest tree, *Elaeocarpus reticulatus*, were blocked with a bitumen paint, numbers of predatory phytoseiid mites per leaf were reduced to 24% of controls during a five month period (Walter and O'Dowd 1992b).

Further circumstantial support for Lundstroem's hypothesis of mutualism comes from the feeding habits of domatium dwelling mites. Most of the mites found in domatia do not belong to plant-feeding taxa but to groups which are chiefly predaceous or fungivorous (O'Dowd and Willson 1989; Walter and Denmark 1991). Through their foraging activities on the leaf surface, predaceous and fungivorous mites could decrease epiphyll loads, fungal parasitism and leaf damage by phytophagous arthropods.

In exchange for these services, the leaf domatia provide a protected microhabitat in an otherwise barren phylloplane landscape. Protection from the elements and from predators may be especially important during the inactive stages, for example the egg stage or during moulting. Pemberton and Turner (1989) showed that *Amblyseius limonicus* (a predatory mite) preferentially lays its eggs in domatia.

Domatia-bearing plants and their mite associates are taxonomically diverse and geographically widespread. Of approximately 290 families of dicots, 28% have representatives with domatia (O'Dowd and Willson 1989). Domatia dwelling mites comprise species from at least 27 families (O'Dowd and Willson 1991). Domatal construction varies among taxa from pits, pockets, and pouches to tufts and very occasionally rolled or folded leaf margins. Plants with domatia occur from the tropics to at least 60°N and 47°S and range in elevation from lowland to montane forest (O'Dowd and Willson 1991). The discovery of fossil leaves with domatia and oribatid mites with arboreal features from the middle-Eocene (37-49 million years old) suggest that mite-domatia associations are ancient (O'Dowd, Brew and Christophel 1991).

The questions addressed in this study

Domatia are frequently used in the taxonomy of African trees (e.g. van Wyk 1983), but beyond this, very little work has been done. This is the first ecological study conducted on the domatia of African plants. It is also the first study which tests the ultimate requirement of Lundstroem's hypothesis of mutualism, i.e. that domatium inhabiting mites benefit plants by playing a role in maintaining leaf hygiene. The study addresses three questions: 1) Are mites associated with the domatia of African trees?; Do domatium bearing plants benefit from the activity of domatium inhabiting 2) fungivorous or 3) predatory mites?

To answer these three central questions, I draw on a number of different sources of information; one source of information (i.e. a survey or experiment) may provide a partial answers to more than one question. Frequent reference is made to other factors which play a role in phylloplane ecology, the most important of these seems to be leaf age, to which an entire section is devoted.

The first part of this study is a census of the arthropods occurring in the domatia and on the leaf surfaces of three forest trees: *Ocotea bullata* has pouch-like domatia (Fig 1 and 2), *Chionanthus foveolatus* has hair tufts in the vein axils (Fig. 3), and *Olea capensis* has no domatia. The main aim of this survey was to determine whether there is an association between mites and the domatia of African plants. *O. capensis* acted as a "control" for *C. foveolatus*. These two species have very similar leaves, barring the presence of domatia in *C. foveolatus*. By comparing the level of mite occupancy on the leaves of these two species, I could determine what effect the presence of domatia has on the size of the mite population. Domatium-less vein axils on the leaves of domatium bearing species acted as "within-leaf controls", for the census of domatia. By comparing the abundance of mites in domatia with the abundance of mites in domatium-less vein axils, I could determine what effect domatia have on the distribution of mites on the phylloplane.



Fig. 1. The domatia of *Ocotea bullata* are visible as bulges on the upper leaf surface

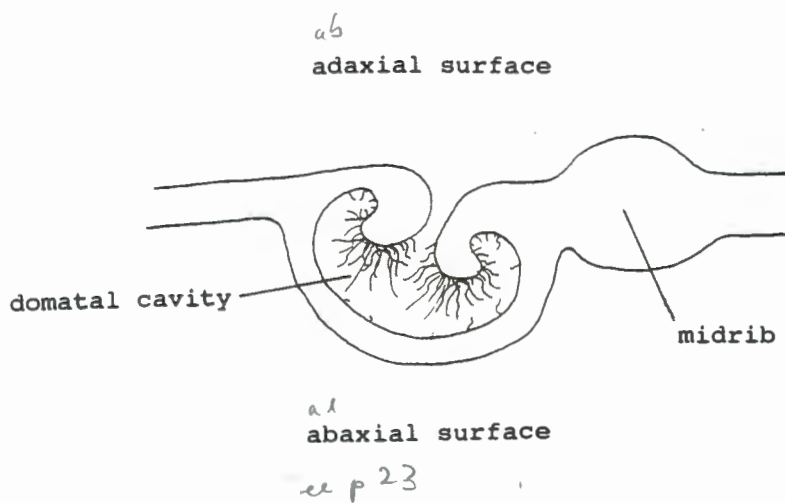


Fig. 2. A crosssection through a domatium of *Ocotea bullata*, showing the trichome bearing lip which guards the entrance to the domatium.

The mites which were collected during the census were identified, and assigned to trophic groups on the basis of their taxonomic affinities. This analysis provides a partial answer to the question concerning the relationship between domatia and leaf hygiene. One measure of leaf condition, namely herbivory damage, was recorded during censusing. This data was used in correlations with the numbers of mites from various trophic groups. If predatory mites benefit the leaf by devouring micro-herbivores and their eggs, then leaves with larger populations of predatory mites should suffer less herbivory damage. This hypothesis was tested in regression analyses. Leaf age is another variable which was recorded during censusing. By analyzing this data, successional changes in the composition of the phylloplane arthropod populations could be studied.

In the second section of this study, I test whether natural variation in the number of fungivorous mites accounts for differences in the abundance of a sooty fungus which is common on the leaves of *C. foveolatus*. This correlative study is an attempt at answering the second question regarding the effect of fungivorous, domatium inhabiting mites.

The third part of this study is a field experiment. I blocked the domatia of *O. bullata* and observed the effect of this treatment on the number of mites per leaf, the level of herbivory damage, and the abundance of phylloplane fungi. This experimental study addresses all three of the proposed questions.

The fourth and final part of this study is a biogeographic analysis. By analyzing the distribution and abundance of domatium bearing trees in the Natal Province (South Africa), I hoped to learn more about the types of habitats in which domatia are an advantage. This information would give insight into the function of domatia.

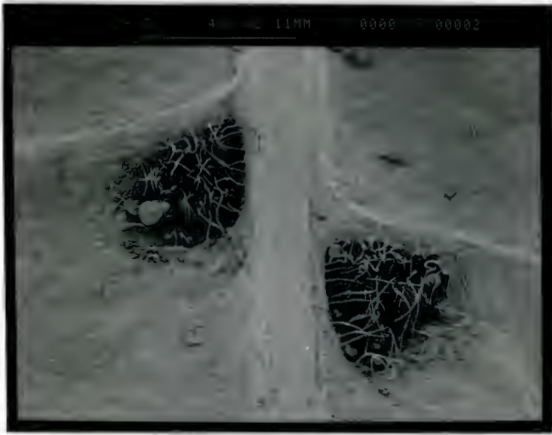


Fig. 3. Two domatia in the vein axils on the abaxial leaf surface of *Chionanthus foveolatus*.



Fig. 4. A domatium on an old leaf which has become choked with the exoskeletons of cryptostigmatid mites.



Fig. 5. An adult cryptostigmatid mite (Family Oribatei), showing the club-shaped bothridial sensuli.



Fig. 6. Two nymphal cryptostigmatid mites belonging to the same species depicted in Figure 5.

Methods

Collection sites

Only "natural" Afromontane forest communities (White 1983) were sampled. *Ocotea bullata* leaves were collected from the eastern slopes of Table Mountain above the Kirstenbosch Botanical Gardens in Cape Town (34°58'45''S; 18°25'30''E 300m). Leaves from *Chionanthus foveolatus* and *Olea capensis macrocarpa* were collected from between Disa stream and "The original Disa stream" in Orange Kloof on the South side of Table Mountain (33°59'45''S; 18°23'45''E 220m). The leaves were collected during July and August.

Recording the abundance of mites and domatia

A fairly consistent association between mites and domatia, is the first requirement of Lundstroem's hypothesis of mutualism. The leaves of *Chionanthus foveolatus* and *Ocotea bullata* were examined to determine whether mites are associated with the domatia of these two African species. Leaf material was collected in a hierarchical fashion: a number of leaves per shoot, several shoots per tree and several trees per species. This allowed me to determine which levels (species, shoot, or leaf) explained most of the variation in either domatium number per leaf or mite abundance using nested ANOVA (Sokal and Rohlf 1984).

To determine what effect the presence of domatia has on the size of the phylloplane mite population, a domatium-less species, *Olea capensis macrocarpa* (henceforth referred to as *O. capensis*), was included in the census. *O. capensis* and *C. foveolatus* occur interspersed in Orange Kloof, where both are common sub-canopy trees ranging in height from 1.7 to 5m. The leaves of *O. capensis* and *C. foveolatus* are very similar; the only noticeable difference being the presence of domatia in the latter (Fig. 7). The censusing methods were the same as for the two domatium-bearing species.

Leaves were placed in separate plastic bags and transferred to a 0° refrigeration room. At this temperature, all arthropods present on the leaves were temporarily immobilized. Material was stored for a maximum of three days before examination. The following leaf attributes were recorded for all three species:

- 1) Leaf length
- 2) Number of domatia
- 3) Leaf rank, i.e. the order of placement relative to the first leaf (*O. bullata*) or pair of opposite leaves (*C. foveolatus* and *O. capensis*), which was assigned rank 1. In later analyses, leaf rank was used as a measure of leaf age. By comparing leaves of different ages, successional trends could be studied.

and for *O. bullata*

- 4) Degree of herbivory damage, rated relative to a series of standard leaves which acted as a yardstick. This information was used to test (through correlation) whether leaves which house more predatory mites suffer less herbivory damage.

For the two species with domatia, domatium-less vein axils were included in the census. If there is an association between mites and domatia, one would expect that more mites would be found inside domatia than inside domatium-less vein axils. On each leaf, the number of vein axils which were examined equaled the number domatia.

Leaves were examined and arthropods counted and collected under a dissecting microscope with a 50X magnification and an optical fibre light source. Where necessary, domatia were dissected. Representative specimens of the mites were collected using the tip of a trimmed paintbrush, and placed in 70% alcohol. Very small mites were preserved on droplets of isopropyl alcohol (25%) which was made into a syrup with sorbitol. The droplets were placed in the inside of the lid of an Ependorf tube. Moist paper in the bottom of the tube prevented the droplet from becoming too tacky. The mites were transferred to the surface of the droplet using a short, sharp-ended hair. Mites were mounted in Hoyer's medium for identification under a compound light microscope.

Scanning electron micrographs of oribatid mites aided identification. Domatia containing mites were 1) fixed in 1% gluteraldehyde in 0.1M phosphate buffer (pH 6.8) for 2 hours 2) rinsed in 0.1M buffer [two changes over 15 min] 3) "post-fixed" in 1% OsO₄ in 0.1M buffer for 1 hour at RT 4) rinsed in 0.1M buffer [two changes over 20 min] 5) dehydrated in an EtOH sequence [50%-100%; two changes each] 6) dried in a critical point drier and 7) coated with gold-palladium.

The mites were assigned to trophic groups on the basis of their taxonomic affinities. Information on the feeding habits of the taxonomic groups was obtained from Walter and Denmark (1991). This information provided a test for Lundstroem's proposal that domatia housed predatory and fungivorous mites. No information was however collected on the relative abundance of various species.

Only fairly crude estimate could be made of the abundance of various trophic groups during censusing. Since immediate identification of the species was not possible, mites were assigned to one of three "types", or trophic groups, on the basis of their gross morphology. These ecological classifications are based on obvious adaptations which suggest a particular mode of feeding. The following three "types" were recognized:

a-type (epiphyll feeders)

Small, short-legged, wrinkled, mouthparts not conspicuous, oval to heart shaped, white. (more or less = Tydeidae)

b-type (predators)

Large, with long hairy legs, first pair usually conspicuously long, fast-moving, large chelicerae, white to pale yellow. (more or less = Phytoseiidae and Stigmaeidae)

c-type (epiphyll feeders/fungivores)

Crab-like, sculptured abdomen, dark brown, slow-moving, mouthparts inconspicuous, bothridial sensillum short and club-shaped (Fig. 5 and 6). (= Nymphal and adult Oribatei, order Cryptostigmata, only one species is included under this type)



Fig. 7. An abaxial view of the leaves of *Chionanthus foveolatus* (left) and *Olea capensis macrocarpa* (right), to show the similarity in leaf morphology.



Fig. 8. Four *Chionanthus foveolatus* leaves with varying amounts of sooty fungus on the adaxial surface. These leaves were used as the standard reference points when the abundance of fungi was assessed.

These crude estimates of the abundance of various trophic groups were used in the analysis of successional patterns and in correlations with different measures of leaf condition. For *O. bullata*, the degree of herbivory damage was regressed against the number of predatory mites (b-type mites) per leaf to test Lundstroem's suggestion that domatia house predatory mites which protect the leaf against microherbivores.

Correlative analysis of mites and fungus on *C. foveolatus*

This section of the study specifically addresses the question regarding the role which mites play in the control of epiphylls. I test whether natural variation in the number of fungivorous mites (c-type mites) accounts for differences in the abundance of a sooty fungus which is common on the leaves of *C. foveolatus*.

The number of fungivorous mites and the amount of leaf fungus on the leaves of *C. foveolatus* was quantified to test for an association. Leaves were collected from the same area as before. The sampling procedure was hierarchical: 12 trees, 4 shoots per tree, and two leaves per shoot (one rank 1 leaf and one rank 3 leaf) were collected. Leaves were stored at 0° for a maximum of 4hrs before censusing.

The amount of fungus present on leaf surfaces was rated relative to 6 standard leaves. Standard leaves were selected so that the amount of fungus increased in a linear fashion from leaf 1 to leaf 6 (Fig. 8). The number of *a*, *b* and *c-type* mites present on each leaf were counted under a dissecting microscope.

The black leaf fungus was identified under a compound microscope with 400X magnification. The fungus was removed from the leaf surface using squares of Selotape^R (7mm X 7mm) which were placed face-down onto the leaf surface and pressed down with a blunt object. The fungal population is lifted from the leaf surface when the squares are peeled off. The squares were mounted sticky-side-up in lactophenol blue.

Experimental manipulation of domatia

If domatia house beneficial predatory and fungivorous mites, then blocking domatia should have the direct effect of reducing the size of the phylloplane mite population, and the indirect effect of elevating the level of herbivory and the abundance of phylloplane fungi. In this section of the study I test whether the long-term inactivation of domatia has these effects on the phylloplane populations and the condition of the leaf.

Experimentation was restricted to a single large *O. bullata* tree (20m in height). On 27/2/91 thirty, young, but fully expanded, leaves that showed no signs of herbivory damage were selected from various heights in the tree. The selected leaves were soft and light green compared to the hard dark green leaves on the rest of the tree. It was estimated that the leaves were at most a month or two old.

The domatia of 10 leaves were filled with white petroleum jelly (Vaseline^R) which was injected into the domatal pockets with a syringe. In 10 control leaves the Vaseline was applied to leaf vein axils which did not bear domatia. The number of axils treated in this way equaled the number of domatia on the specific leaf. The immigration of mites from nearby leaves was hindered by a barrier of Vaseline^R which was applied around the petiole of experiment and control leaves. An additional 10 control leaves were left untreated. The leaves were marked with coloured wool which was tied around the shoot just above the petiole.

Leaves were checked after 45, 100 and 540 days. The degree of leaf damage due to herbivory was rated relative to standard leaves.

On the 28/8/92 (18 months later) the leaves were collected, bagged and transferred to a 0° refrigeration room. The tree had lost a branch during a windstorm, so only 5 of the experiment leaves, 6 control leaves and 8 untreated leaves could be found. Censusing of mites started immediately, and finished a few hours later. All mites were collected and preserved in 70% alcohol for later identification.

An adaptation of a technique described by Oliver (1978) was used to remove all epiphylls from the leaf surface so that these could be censused under a compound light microscope. 400ml of 2% pure agar was kept in the liquid state at 65°C in a wide glass beaker on an electric hot plate. Four drops of Tepol^R (a wetting agent) were added to the agar and the beaker was sealed to prevent evaporation. Leaves were briefly submerged in the liquid agar. The leaf was rotated while excess agar dripped off; this ensured an even coating. Agar coated leaves were suspended from their petioles in a drying rack which was transferred to a air-circulated drying oven set at 50°C. After 5 minutes, the agar dries to a very thin, entirely transparent film which coats the entire leaf surface. After 7 minutes, the agar film starts to lift off the leaf surface in a continuous sheet.

Six "quadrats" measuring 1cm X 1cm were cut from the agar film covering each leaf; 3 from the upper and 3 from the lower surface. The quadrats were evenly spaced along a transect running midway between the rachis and the leaf margin. The first "quadrat" was cut from the leaf-tip area and the last from the basal area. On each surface two of the three "quadrats" were taken from one side of the rachis and the remaining one from the other side. The squares of agar film were mounted in lactophenol blue.

Prior to sampling, similar agar membranes were prepared from leaves collected from the same tree. Sections of these were photographed using a Zeiss^R compound microscope fitted with a camera, Ilford Delta 200^R film and a green filter. The photographs were arranged along a linear scale from 0 to 9 on the basis of the amount of fungus present. These photographs acted as the reference points during sampling.

A magnification of 200X was used both for photography and sampling. At this magnification, the area between the camera field of view indicators (which are engraved on the eyepiece) measures 0.46 X 0.69mm. Other settings, such as aperture size, which might affect the extent to which the mycelium is visible were kept constant throughout.

Each "quadrat" was subsampled to assess the amount of fungus present. The stage control was used to move the field of view along a transect which criss-crossed the agar film. The amount of fungus present within the camera field of view indicators was assessed at intervals of 0.5mm. 20 subsamples were taken per microscope slide (quadrat).

To evaluate the effectivity of the fungus removal technique, SEM micrographs of the fungi on *O. bullata* leaf surfaces were taken to compare with the agar preparations. Small sections of the leaf were placed on a gauze stand above a shallow dish containing a few drops of osmiumtetroxide solution. The gauze stand and dish were covered with a glass bell and left in a fume cupboard for a week. The leaf fragments were coated with gold-palladium and viewed with a S200 scanning electron microscope.

Fungi removed from the leaf surface using the agar technique appeared undamaged and generally very similar to in situ fungal populations viewed under the scanning electron microscope (Fig. 9). This indicates that the agar technique is very effective in the removal of phylloplane fungi.

Method of biogeographic analysis

In this section I analyze the distribution of domatium bearing trees in relation to environmental variables. A data set listing tree distributions for the Natal Province was used to produce a density graded distribution map of the occurrence of domatia bearing trees. The data set contained 674 digitized distribution maps taken from Moll (1981). Data for all 156 of the quarter-degree squares covering Natal was available. Presence throughout a square was scored as 10; trees with distribution ranges covering only one half of a square were scored as 5, etc. For each square the total score for trees with domatia was expressed as a percentage of the score for all trees. Thus, the number of tree species per grid did not affect the analysis.

Trees were considered to have domatia if this was obvious from the drawings in Palgrave (1977) or Moll (1981); or if the text in either of these books referred to hair

tufts or sunken pockets in the vein axils. Although species with domatia may have been missed, all those with prominent domatia were included.

The data set did not include all the Natal trees, however, absenteeism was random with respect to domatal presence or absence, and should not affect the pattern. The tree species which were included in the analysis are listed in Appendix 1.

Results

Description of domatia

The domatia of *Ocotea bullata* are the most characteristic feature of the tree, hence the specific epithet "*bullata*". The domatia are located in the axils of about 3 of the proximal side veins where they join the midrib of the leaf (Fig. 1). The domatia protrude like blisters (or bullae), which may be 4mm high, above the adaxial surface of the leaf. On the under-surface of the leaf the domatium has a lipped, slit-like opening 3mm long, guarded by a dense fringe of non-glandular hairs (Fig. 2).

The domatia of *Chionanthus* are conspicuous tufts of non-glandular hair in shallow depressions in most of the vein axils along the leaf midrib (Fig. 3). The hair tufts measure 1 to 2mm across at the widest part. On the upper surface, only slight bulges are visible.

Distribution and abundance of leaf domatia

Domatia are consistently present on the leaves of both *O. bullata* and *C. foveolatus* (Table 1).

Table 1. Mean, minimum, maximum and standard deviation for number of domatia per leaf in *O. bullata* and *C. foveolatus*.

Species	Mean	Std.	Min.	Max.	n
<i>O. bullata</i>	3.44	1.187	1	6	102
<i>C. foveolatus</i>	7.18	2.23	4	11	56

The distribution of variation in the number of domatia per leaf differs considerably between the two species (Table 2 and 3). In *C. foveolatus* there is a lot of variation in the number of domatia per leaf between different trees while there is little variation between shoots within a tree. In *O. bullata*, there is very little variation between trees, while there is a lot of variation between the shoots of one tree.

Table 2. Partitioning of variance in number of domatia per leaf among trees, shoots and leaves of *C. foveolatus*.

Source of variation	Sum of squares	D.f.	Mean square	% of variation explained →
Tree	84.66	2	42.33	41.56
Shoot	39.56	9	4.40	6.21
Leaf	107.25	36	2.98	52.23

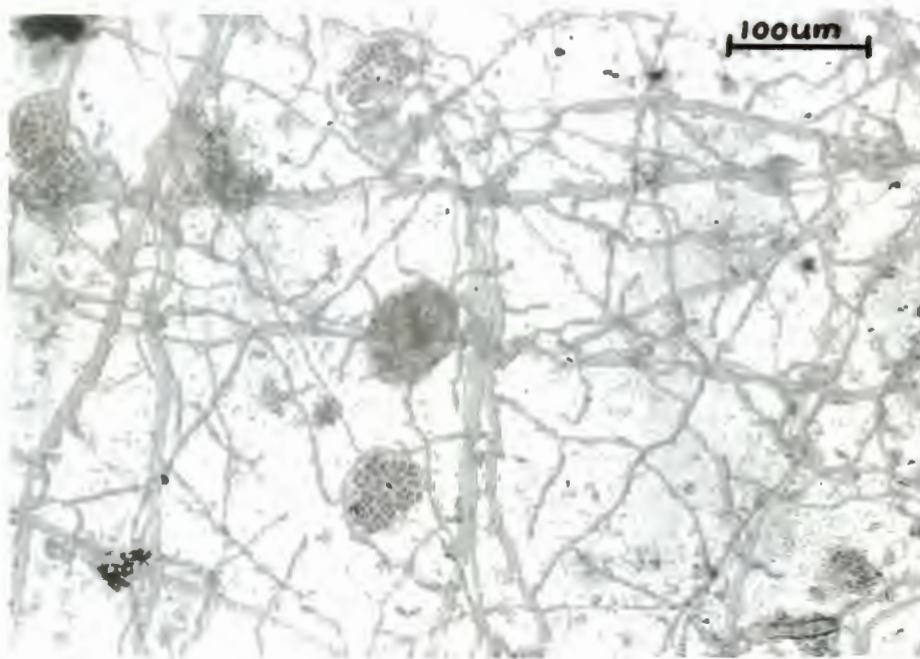


Fig. 9. Fungi removed from the leaf surface of *Ocorea bullata* using the agar technique and viewed under a compound microscope (bottom) looks very similar to fungi photographed in situ (top), indicating that the agar technique is successful in the removal of phylloplane fungus. Notice the clusters of conidia in the bottom photograph.

Distribution and abundance of mites in domatia

Most of the domatia of *C. foveolatus* and *O. bullata* contain evidence of mite occupation (Table 5). All life-history stages including eggs were commonly present and large numbers of mite exoskeletons were often trapped in the domatal hairs. Mites are also the most abundant arthropods in domatia (Table 6). The association between mites and domatia is not purely coincidental; in both species domatia harbour many more mites than neighbouring domatium-less vein axils (Table 7). The hairy pockets in the vein axils of *C. foveolatus* and *O. bullata* truly earn the name "acrodomatia" - little mite houses.

Table 5. The proportion of the domatia and leaves occupied by mites. Leaves of all ranks are included. Evidence of previous mite occupation includes exoskeletons, dead mites and mite eggs.

	Species	
	<i>O. bullata</i>	<i>C. foveolatus</i>
Proportion of leaves which harbour mites in domatia	0.77	1
Proportion of leaves with mite evidence in domatia	0.82	1
Proportion of domatia occupied by mites	0.36	0.62
Proportion of domatia with evidence of mite occupation	0.51	0.97

Table 6. Frequency of mite occupancy in leaf domatia (values in parenthesis indicate number of arthropods, leaves or domatia examined).

Species	Mites as percentage of arthropod occurrences	Number of mites per leaf	Number of mites per domatium
<i>C. foveolatus</i>	99 (731)	13.25 (56)	< 1.95 (402)
<i>O. bullata</i>	80 (270)	1.95 (101)	0.62 (347)

Table 7. Percentage of vein axils which harbour mites when a domatium is present (Domatia) or absent (Axil). The number of vein axils or domatia examined is given in parenthesis.

Species	Domatia	Axils
<i>O. bullata</i>	36.02 (347)	0.29 (347)
<i>C. foveolatus</i>	62.44 (402)	3.16 (285)

There are significantly more mites on the leaves of *C. foveolatus* (rank1 = 6.48, rank3 = 8.8) than on the leaves of a co-occurring species, *O. capensis*, which lacks domatia (rank1 = 0.68, rank3 = 0.88)(Table 8). The number of mites per leaf varies more between different species (with and without domatia) than between trees of one species, ranks within one tree or leaves within a rank. Thus, the presence or absence of domatia accounts for a very large proportion of the variation in the number of mites present on leaves.

Table 8. A tabulation of the percentage of variation in mite numbers which is contributed by the following nested sources of variation: species (*C. foveolatus* & *O. capensis*); individual trees within species; leaf ranks (1 & 3) within trees and leaves within ranks.

Source of variation	Sum of squares	D.f.	Mean square (explained)	% of variation
Species	2044	1	2044	43.55
Trees	1558	18	86	9.26
Ranks	898	20	44	10.91
Leaves	2446	120	20	36.27

Leaf length and the number of domatia per leaf explain significant proportions of the variation in mite numbers on the leaves of *C. foveolatus*. To minimize the effect of leaf age, each analysis included only leaves of the same rank (Table 9).

Leaf ranks could not be analyzed separately in *O. bullata*. When all ranks are taken together the correlations are not significant, although there is a positive relationship between the number of mites and leaf length, and between the number mites and the number of domatia. Variation in leaf age probably obscures the relationship between these variables resulting in the lack of significance.

Table 9. A linear regression model with number of mites per *C. foveolatus* leaf as the dependant variable and number of domatia and leaf length as the independent variables. Separate analyses were run for rank 1 and rank 3 leaves (d.f. in parenthesis).

Rank	R-squared (%)	Probability level	Slope	Intercept
Domatia				
rank 1	13.59 (47)	<0.005	1.07	0.77
rank 3	8.23 (47)	<0.025	0.58	6.15
Length				
rank 1	13.66 (47)	<0.005	0.17	-6.91
rank 3	13.10 (47)	<0.01	0.17	-4.60

All in all, the results indicate that there is a strong association between mites and domatia. Mites in all stages of development are common inside domatia. Leaves with domatia have more mites; leaves with more domatia have more mites; and vein axils with domatia attract more mites than vein axils without.

The taxonomic and ecological classification of mites

Ten species of mites were recovered from the domatia of *O. bullata*. These taxa all belong to groups which are potentially beneficial to the plant (Appendix 2). The predatory taxa, Stigmeidae and Phytoseiidae were the most common, while no herbivorous mites were present in the domatia.

Although no mites were identified from the domatia of *C. foveolatus*, the relative abundance of the three "types" was recorded. The *c*-type, which comprises only one species constituted 88% of the individuals recovered from the domatia. This species, belongs to the order Cryptostigmata in the family Oribatidei (Oribatei). Arboreal

members of the Oribatidei are known to feed primarily on fungi and other epiphylls (Walter and Denmark 1991). B-type mites, which are characterized by having adaptations for hunting, accounted for a large proportion of the remaining mites found in the domatia of *C. foveolatus*.

The trophic classification of mites found in domatia lends circumstantial support to the proposed mutualistic relationship between mites and plants. There is further circumstantial evidence suggesting that domatium inhabiting mites benefit the leaves on which they live. Many of the leaves of *O. bullata* suffer extensive herbivory damage in the form of nicks taken out of the leaf margin. There is a significant negative correlation between the degree of herbivory damage to leaves (dependant variable) and the numbers of predatory mites (b-type mites) (independent) ($R^2 = 3.24\%$, d.f. = 100, $P < 0.05$, slope = -0.66, intercept = 3.74; Fig. 10). The abundance of other mites does not appear to effect or be effected by the degree of herbivory damage.

Successional patterns in the abundance of mites

The abundance of mites differs considerably between leaves of different rank, indicating that leaf age is a very important variable to consider in the study of mite-plant mutualism. In *O. bullata* the number of mites per leaf differs more between leaves of different rank than between leaves from different trees or shoots (Tables 10 and 11). In *C. foveolatus* the partitioning of variance in mite numbers differed considerably for predatory mites (*b*-type, Phytoseiidae and Stigmaeidae) and epiphyll feeders (*c*-type, Cryptostigmata) (Table 11), but for both leaf age is an important source of variation.

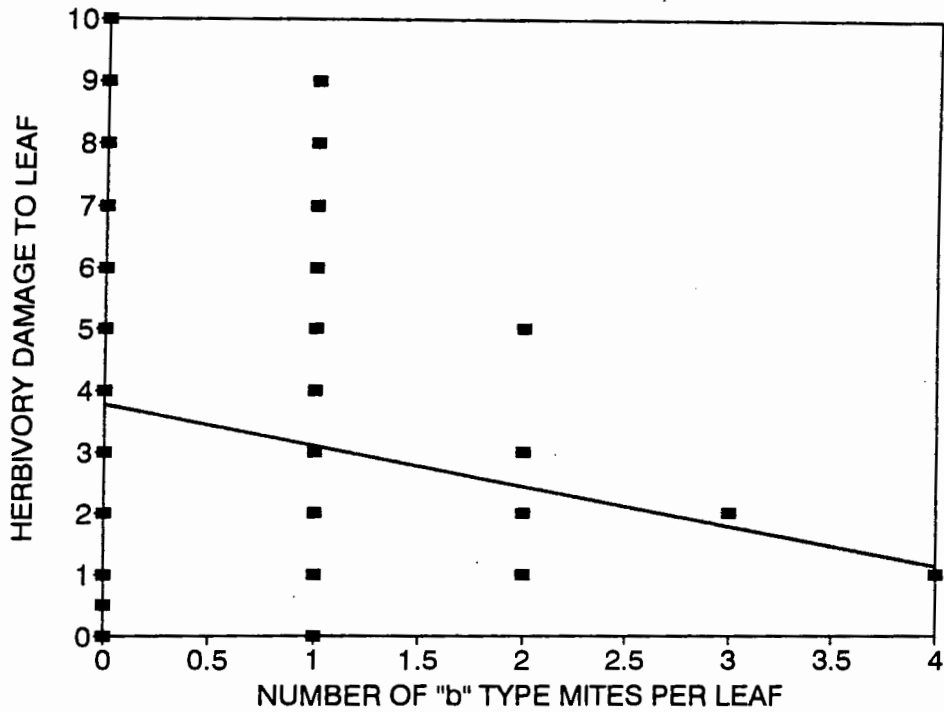


Fig. 10. There is a significant negative relationship between the number of "b" type mites (predatory phytoseiids and stigmatids) and the degree of herbivory damage to the leaves of *Ocotea bullata* ($r = 0.18$, slope = -0.66 , $df = 99$, $p < 0.05$).

Table 10. Partitioning of variance in the number of mites per leaf among trees, shoots and leaves of *O. bullata*.

Source of variation	Sum of squares	D.f.	Mean square (explained	% of variation
Tree	14.19	2	7.09	1.88
Shoot	64.56	12	5.38	12.31
Rank	188.00	60	3.13	85.82

Table 11. Partitioning of variance in the number of mites per leaf among trees, shoots and leaves of *C. foveolatus*. Values for *c*-type mites (epiphyll feeding Cryptostigmata) and *b*-type mites (predatory phytoseiids and stigmatoids) are listed separately.

Source of variation	Sum of squares	D.f.	Mean square (explained	% of variation
Tree				
Epiphyll feeders	3180.79	2	1590.40	66.37
Predators	0.04	2	0.02	0.00
Shoot				
Epiphyll feeders	475.94	9	52.88	0.96
Predators	3.38	9	0.38	12.82
Leaf (Rank)				
Epiphyll feeders	1702.75	36	47.30	32.67
Predators	8.50	36	0.24	87.18

In *C. foveolatus* rank 1 leaves have fewer oribatid mites (*c*-types) and more phytoseiid and stigmatid mites (*a*-types) than leaves of higher rank (Fig. 11). The proportion of oribatid mites which are in the nymphal stage is also lower on rank 1 leaves (Fig. 12). However, the variation in the numbers of oribatids on leaves of different rank is not significant in a one way ANOVA ($F = 1.157$, $df = 47$, $P = 0.33$), and all ranks are considered homogeneous in a selection of multiple range tests (Scheffe, Bonferroni, Newman-Keuls, Duncan, LSD and Tukey)(Zar 1984). However, a one way analysis of variance picked up statistically significant variation in the numbers of predatory mites on leaves of different ranks ($F = 3.414$, $df = 47$, $P = 0.0255$). The Least Significant Difference Test (a method of multiple comparison) (Zar 1984) showed that there are significantly more predatory mites on rank 1 leaves than on leaves of higher ranks. There were no significant differences in the number of predatory mites on leaves of rank 2 to 4.

Figure 13 is a graphic depiction of mite occupancy of *O. bullata* leaves of ranks 1 to 7. There appears to be no clear successional pattern as was found in *C. foveolatus*. It seems probable that the identification of trophic groups was too crude to pick up successional changes in the composition of the phylloplane mite population.

Fungus mite correlations in *C. foveolatus*

Lundstroem (1887) suggested that domatium inhabiting mites may benefit the leaf by feeding on harmful epiphylls. I tested this suggestion by correlating the abundance of fungus and fungivorous mites on the leaves of *C. foveolatus*, and found no apparent interaction.

The most common epiphyll on the leaf surfaces of *C. foveolatus*, is a black leaf fungus. The fungus was identified as a member of the genus *Phialophora* (Ainsworth *et al.* 1973). Characteristic of this genus are the non-septate conidia which are produced singly by monophialidic conidiogenous cells. The conidiogenous cells differ from the vegetative hyphae in being slightly swollen (Fig 14 and 15).

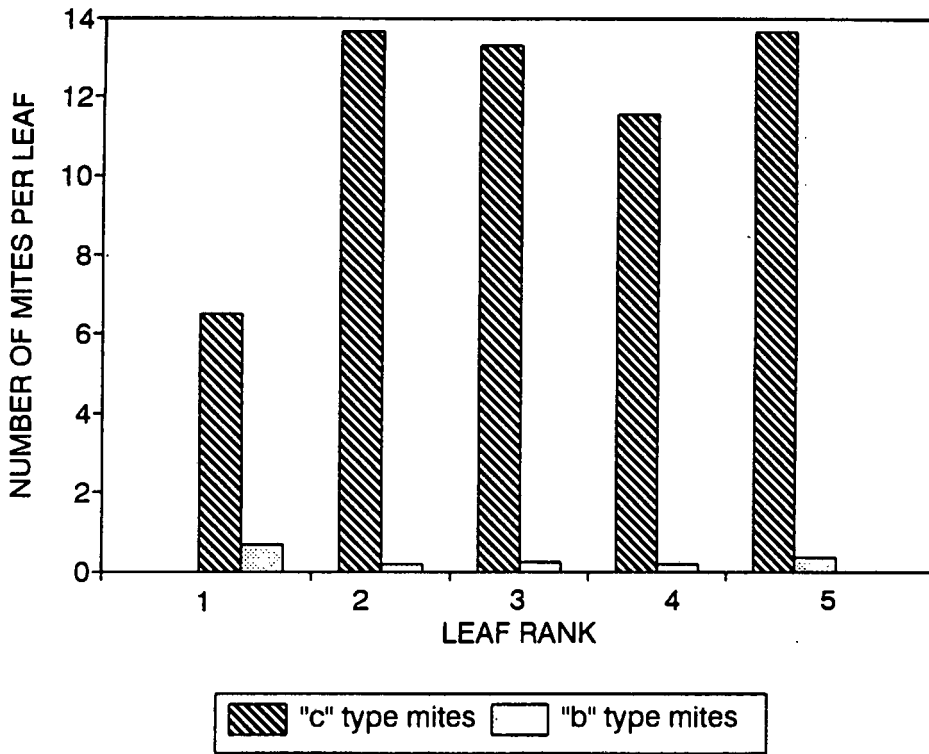


Fig. 11. Young leaves (rank 1) of *Chionanthus foveolatus* differ from older leaves in having larger numbers of predatory mites (b type; phytoseiids and stigmatids) and fewer fungivorous mites (c type; cryptostigmatids).

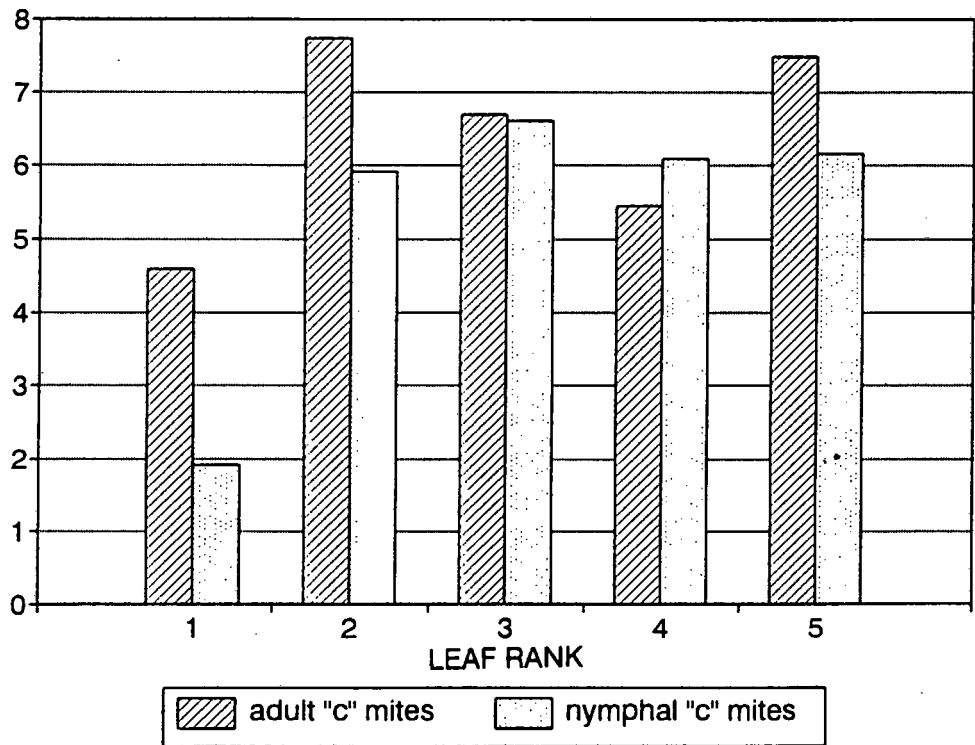


Fig. 12. On the young leaves (rank 1) of *Chionanthus foveolatus* a larger proportion of the 'c' type mites (Cryptostigmata) are adults.

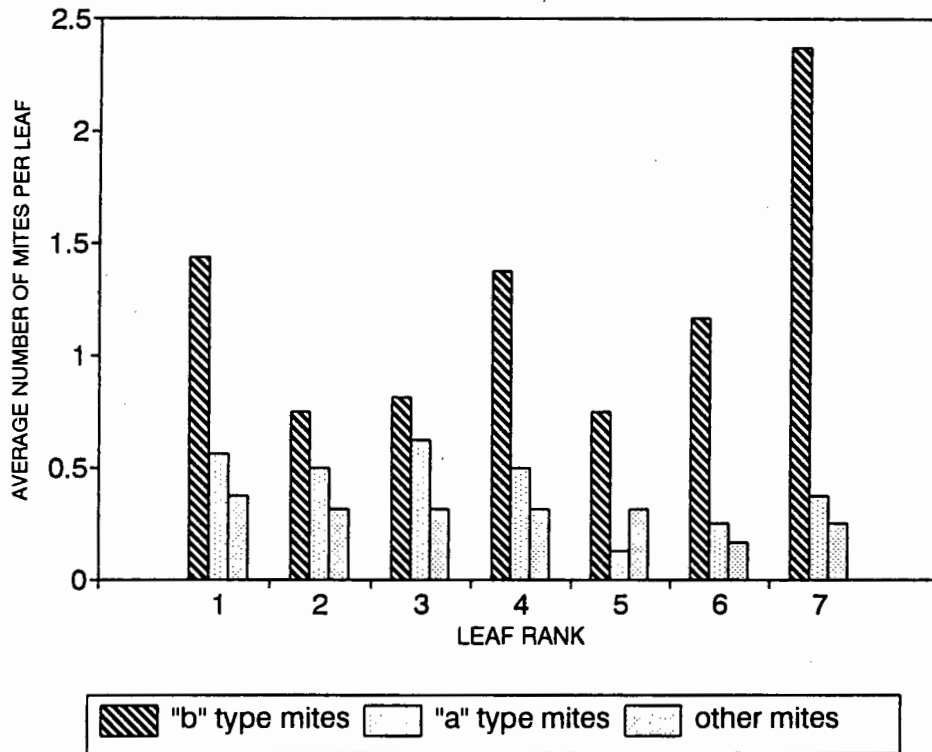


Fig. 13. There is no obvious successional change in the composition or size of the mite populations on the leaves of *Ocotea bullata*.

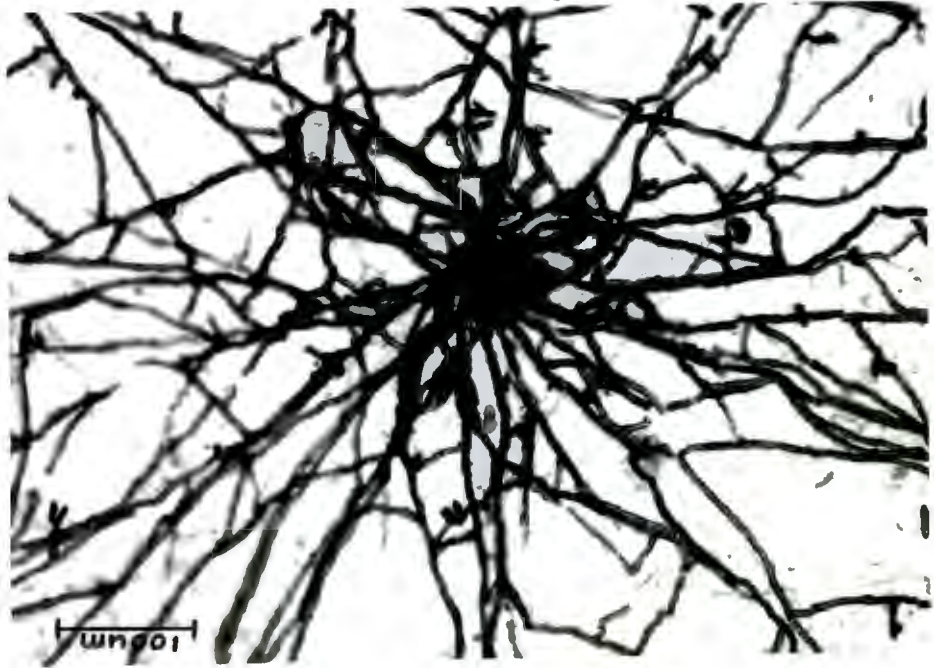


Fig. 14. The black hyphae of *Phialophora* radiate outwards from the point of germination.

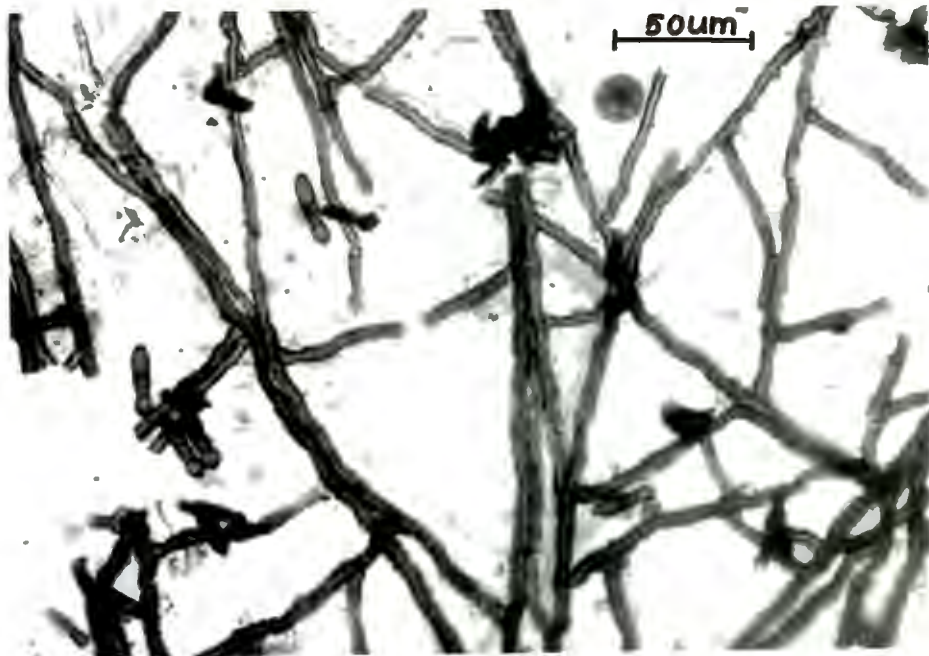


Fig. 15. Five conidiogenous cells with non-septate conidia borne on vegetative hyphae.

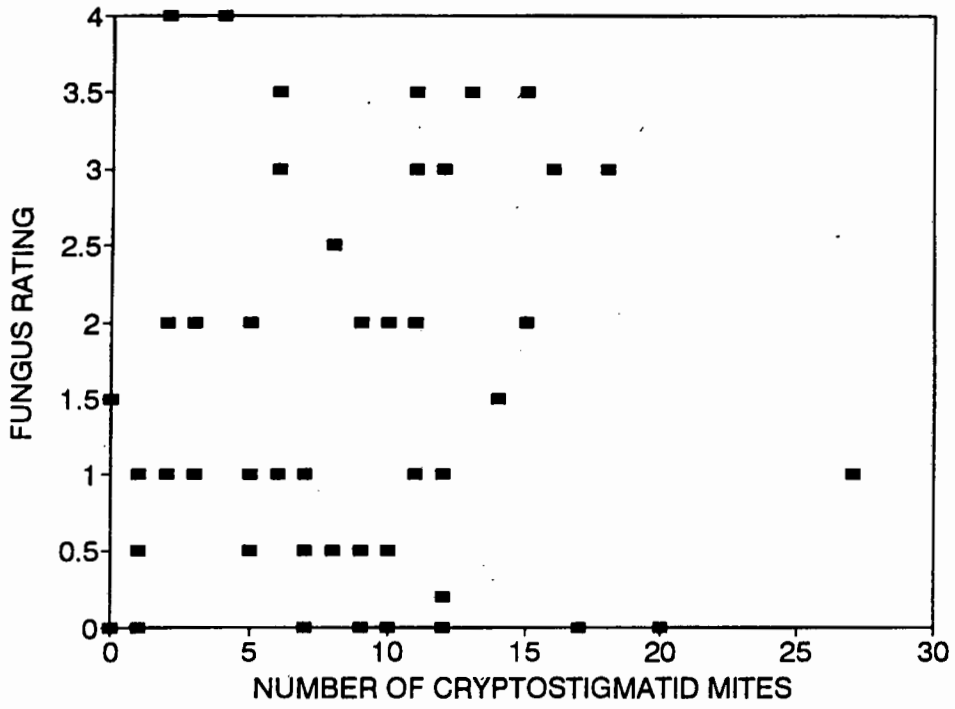


Fig. 16. There is apparently no relationship between the abundance of the fungus *Phialophora* and the number of fungivorous cryptostigmatid mites present on the leaf.

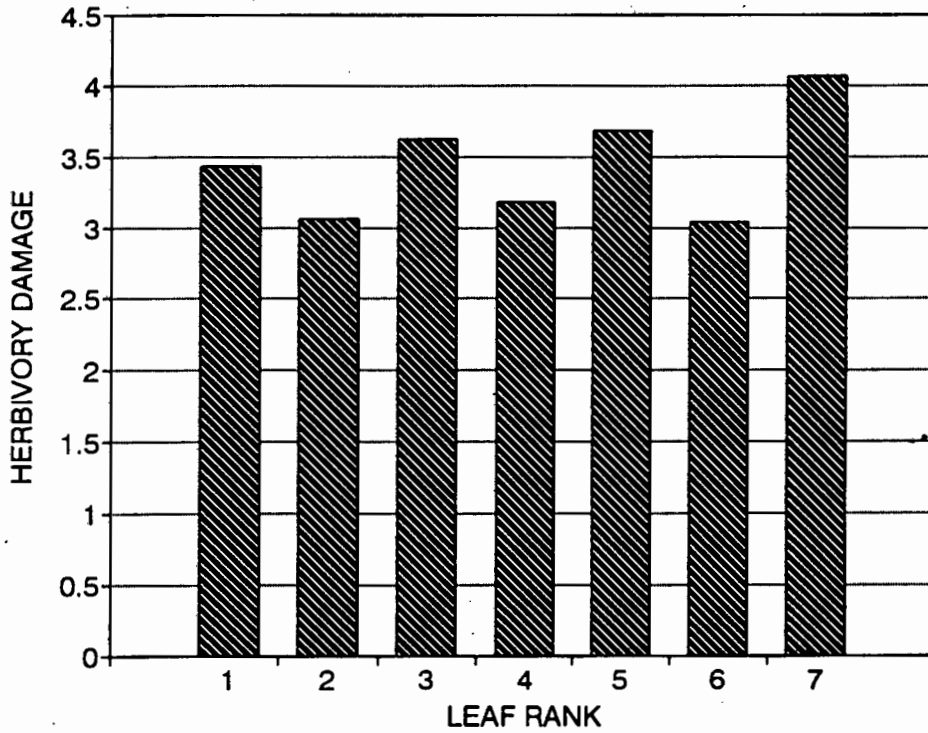


Fig. 17. The degree of herbivory damage, which consists of nicks taken out of the leaf margin, does not increase with increasing leaf age (rank)

Slow moving, sturdy cryptostigmatid mites comprise 88% of the individuals in the domatia of *C. foveolatus*. Like other Arboreal oribatids, the cryptostigmatid mites almost certainly feed on epiphylls.

The abundance of both cryptostigmatids (Fig. 11) and *Phialophora* increases with increasing leaf age (rank). In a two-sample analysis, the difference in the amount of *Phialophora* on rank 1 and rank 3 leaves is highly significant (rank1 mean = 0.01, rank3 mean = 1.45, $t = -7.91$, d.f. = 94, $P = 4.7E-12$). The difference between the number of cryptostigmatids on rank 1 and rank 3 leaves is not as great (rank1 mean = 5.93, rank3 mean = 8.64, $t = -1.93$, d.f. = 94, $P = 0.057$). These results emphasize the importance of considering leaf age in the study of mite-plant interactions.

Although most of the variation in the amount of fungus on leaves does result from differences in leaf rank, there is still a great deal of variation within ranks (Table 12).

Table 12. The partitioning of variation in the abundance of *Phialophora* among nested sources of variation.

Source of variation	Sum of squares	D.f.	Mean square explained	% of variation
Trees	16.21	11	1.47	0
Ranks	65.04	12	5.42	66.61
Leaves	43.46	72	0.60	33.39

Contrary to expectations, the variation in the amount of *Phialophora* on leaves of the same ranks can not be accounted for by variation in the number of oribatid mites per leaf ($R^2 = 0.46\%$, d.f. = 47 for rank 3 leaves). The scattergram in Figure 16 shows that there is apparently no relationship at all between the abundance of *Phialophora* and

the number of oribatid mites on rank 3 leaves. Rank 1 leaves have too little *Phialophora* for a meaningful analysis.

A comparison of the partitioning of variation in the abundance of mites and fungus, lends further support to these findings. Differences between trees account for a large proportion of the variation in mite numbers (Table 11); some trees have many mites per leaf (largest mean = 14.5), while others have few (smallest mean = 2.75). In contrast, the abundance of *Phialophora* does not differ between trees (Table 12). It seems that the abundance of cryptostigmatid mites and the abundance *Phialophora* varies independently.

Experimental manipulation of domatia

I blocked the domatia of a number *O. bullata* leaves and observed the effect of this treatment on the number of mites per leaf, the degree of herbivory damage and the abundance of fungi.

Application of Vaseline^R to the domatium-less vein axils of control leaves had no effect on mite abundance after 18 months. Very few were present to be entombed on the newly flushed leaves and sufficient time was allowed for the populations to recover. 18 months after treatment mite abundance on mock-blocked leaves (mean = 8.25) was not significantly different from that on untreated leaves (mean = 7.7)(probability of exceeding $Z = 0.835$). However, the blocking of domatia on experiment leaves resulted in a near significant reduction in the number of mites on the leaves (non-parametric two sample analysis: average rank for control leaves = 7.7 (based on 7 values), for experiment leaves = 4.7 (based on 5 values), one tailed probability of exceeding $Z (0.137) = 0.068$).

Mite exclusion treatments (experiment, control and untreated) did have a significant effect on the degree of herbivory damage suffered by leaves after 18 months (F-ratio = 11.8, d.f. = 19, $P < 0.0006$), but not after 100 or 45 days. Multiple range tests revealed that leaves with blocked domatia suffered significantly greater herbivory damage than either control or untreated leaves. Control leaves suffered insignificantly more herbivory damage than untreated leaves.

After 18 months, fungus was equally abundant on experiment as on control leaves, despite the reduction in mite numbers on experiment leaves. In a nested ANOVA, positions on the leaf (top, bottom; tip, middle, base) accounted for most of the variation in the amount of fungus, while treatment (experiment, control) accounted for none (Table 13). Even within the 1cm X 1cm quadrats, the distribution of the fungus was patchy; differences between individual estimates ("subquadrats" measuring 0.46 mm X 0.69mm) contributed the remaining portion of the variation. No mite induced damage was visible on mycelia collected from control or experiment leaves.

Table 13. The relative contribution of nested sources of variation to the variability in the amount of fungus in 0.46 mm X 0.69mm "subquadrats" on the leaves of *O. bullata*. Subquadrats are nested within quadrats measuring 1cm X 1cm. These are located in one of six positions on the leaf. Positions are permutations of: adaxial, abaxial; tip, middle and base. "Treatments" are experiment (blocked domatia) and control (blocked vein axils).

Source of variation	Sum of squares	D.f.	Mean square (explained)	% of variation
Treatment	10.12	1	10.12	0
Leaf	711.91	8	88.99	0
Qadrat position	4719.53	50	94.39	74.68
"Subquadrats"	1787.17	1080	1.65	25.32

Results of the biogeographical analysis

The result of the biogeographical analysis is depicted in Figure 22.

Discussion

The distribution and abundance of domatia

The domatia of *C. foveolatus* and *O. bullata* are consistent enough in their occurrence to be used as diagnostic features in both species (Moll 1981). Differences between leaves, rather than shoots or trees, account for the majority of the variation in the number of domatia per leaf for both species (Table 2 & 3). This is consistent with

reports from Australia where O'Dowd and Willson (1989) found that for 18 out of 24 species the majority of the variation lay among leaves.

O. bullata has few domatia per leaf (mean = 3.4) compared to *C. foveolatus* (mean = 7.1) and a long list of species from Australia (O'Dowd and Willson 1989). The number of domatia per leaf in *C. foveolatus* is closer to the Australian average. What *O. bullata* may lack in quantity, it makes up for in quality. In both species the domatia are hollow, hairy depressions in the vein axils of the abaxial surface (Fig. 2 and 3). However, in *O. bullata* the depression is much deeper and its entrance is guarded by a thickened trichome bearing rim. There are probably few other plants in the world in which the domatia are as conspicuous and elaborate.

O'Dowd and Willson (1989) report that in some species the number of domatia per leaf is correlated with leaf area or the number of major vein axils per leaf ($P < 0.05$ in 17 and 18 out of 34 species, respectively). I found that in both *C. foveolatus* and *O. bullata* the number of domatia per leaf was positively correlated with the length of the leaf (Table 4). This is hard to explain since the number of domatia seems to be fixed at an early stage of ontogeny. A correlation between the two variables requires that leaf size is also predetermined.

It has been suggested that domatia are galls induced by mites (Jacobs 1966). Some herbivorous mites do induce the production of deep pocket-like galls in the vein axils of leaves. However, the interaction between gall-mites and leaves is likely to vary considerably in its intensity in both space and time. The consistency with which domatia occur on *C. foveolatus* and *O. bullata* suggest that domatia are inherent properties of these species, which, unlike galls, are not induced by mites. In *O. bullata* the domatia are already clearly visible in very young leaves which are unlikely to have been exposed to gall forming or other mites.

Mite-domatium associations

The results of the mite census indicate that there is a strong association between domatia and mites. This finding extends the list of areas from which mite-domatium associations have been reported to include the African continent. The frequency of mite occurrence falls within the range reported from other continents (Table 14).

Table 14. Frequency of mite occupancy of domatia at various geographical locations. Occupancy is expressed both on the basis of domatia (% of domatia occupied) and on the basis of leaves (% of leaves with at least one occupied domatium). The number of plant species sampled in each area are listed under "n". (After O'Dowd and Willson 1991)

Region	Domatia	Leaves	n
Illinois, USA	59	100	25
California, USA	23	50	12
Florida, USA	64	99	1
Hawaii, USA	23	40	15
Costa Rica	10	30	1
Papua New Guinea	20	63	4
Queensland, Aust.	60	90	19
Victoria, Aust.	36	60	4
New Zealand	38	63	12
<i>Ocotea bullata</i>	36	77	-
<i>Chionanthus foveolatus</i>	62	100	-

Although not as common as mites, other arthropods are also present in domatia. It is surprising that the domatia of *O. bullata* contain a much higher proportion of non-mite arthropods than those of *C. foveolatus* (Table 6). The only non-mite inhabitants found in the domatia of *C. foveolatus* were 3 hoverfly larvae. I expected that the shallow "low-cost" domatia of *C. foveolatus* (Fig. 3) would be less effective at excluding (presumably) unwanted guests. However, it seems that the luxurious domatia of *O.*

bullata are a greater attraction. Thrips (Thysanoptera) and scale insects (Coccoidea), which comprise, respectively, 7% and 4% of the total domatal fauna, are the most abundant non-mite animals in the domatia of *O. bullata*. The thrips were common on the leaf surfaces. They seemed to gain access to the domatia by eating the fringe of hair which guards the entrance to the domatium (Fig. 2). The damage caused by thrips not only decreases their suitability as shelters for mites, but allows access by other harmful insects which would normally have been excluded. Scale insects are only present in domatia in which the guard hairs have been grazed off. Scale insects have sucking mouthparts and are unable to do this kind of damage. It seems that they rely on thrips to break the defences of the domatium.

The raised trichome covered lips guarding the entrance to the domatia of *O. bullata* keep out more than unwanted insects. When a number of leaves were examined after a rainstorm, it was found that domatia in which the fringe of hair has been damaged were occasionally flooded, while in undamaged domatia the guard hairs kept the water out.

According to Beattie (1985) the quality of ant-domatia in *Acacia* thorns can in part be defined by the quality of the entrance hole. A superior hole prohibits access by enemies but permits an internal circulation of air at the optimal temperature and humidity. My observations in *O. bullata* suggest that features of the entrance hole are equally important in mite-domatia.

The high levels of mite occupancy in the domatia of *C. foveolatus* and *O. bullata* fulfill the first requirement of Lundstroem's hypothesis of mite-plant mutualism. Two lines of evidence are still needed. It needs to be shown 1) that the use of domatia enhances the fitness of the mites and 2) that the activity of the mites enhances the fitness of the domatia bearing plant.

The use of domatia which enhances the fitness of mites

A number of lines of evidence suggest that the mite domatium association is more than coincidental; mites specifically make use of domatia, and in so doing derive a great benefit from their presence on the leaf.

The addition of a few trichomes to a vein axil can provide a sheltered, humid microhabitat which contrast with the barren leaf environment. On domatium-less leaves, mites are often found sheltering in the vein axils. However, when domatia are present, mites greatly prefer the shelter which they provide to the alternative shelter provided by domatium-less vein axils (Table 7). The humid microclimate of domatia is probably part of the attraction. With their proportionately large surface areas, mites are particularly vulnerable to desiccation and are usually only found in moist environments. The humidity inside the sunken, trichome lined domatia is probably much higher than that on the leaf surface.

In addition to the protection provided against the physical environment, domatia also offer protection against large arthropod predators such as spiders. The slit-like trichome-lined entrance to the domatia of *O. bullata* may serve the dual purpose of keeping a favourable microclimate in, and large mite predators out.

The presence of large numbers of mite exoskeletons in the domatia of both species indicates that mites seek out the shelter of domatia before ecdysis (Fig. 4). Moulting mites are temporarily immobilized so protection from predators will be particularly important. Before the proteins in the new exoskeletons have become tanned the mites are also more vulnerable to desiccation. The egg stage is another vulnerable period in the life of a mite. Eggs are immobile and vulnerable to predation and desiccation. Thus it is not surprising that mite eggs are common in domatia.

The fact that leaves with domatia have a ten times more mites than leaves without, is a further indication that mites benefit greatly from the presence of domatia. In their external morphology the leaves of *O. capensis* differ from the leaves *C. foveolatus* only in the absence of hair tufts from the vein axils (Fig. 7). In the study area, the crowns of

these two species were often in contact, yet the leaves of *O. capensis* support a much smaller mite populations.

The huge effect which a subtle difference in leaf morphology has on the phylloplane mite populations, was convincingly illustrated in a "natural experiment". On two of the leaves collected from *O. capensis* the number of cryptostigmatid mites was an order of magnitude greater than on other leaves. These two leaves had been damaged along the midrib on the abaxial surface. In response to the damage, the leaves produced domatium-like calluses around which the mites were clustered (Fig. 18). The subtraction of domatia has the opposite effect. In *O. bullata* the mite population on leaves with blocked domatia was half that of control leaves. It is apparent that mites benefit greatly through their use of domatia, and that the presence of domatia or domatium-like structures on the phylloplane encourages mites to live and reproduce on the leaf.

Intraspecific comparisons give a more subtle indication of the effect of domatia on the mite population. Differences in the number of domatia per leaf account for a significant proportion of the variation in mite numbers between *C. foveolatus* leaves of the same rank (Table 9). The same is true for leaf length (Table 9), and since these variables are correlated (Table 4) it is not possible to identify the causal factor. Nevertheless, interspecific comparisons and experimental studies convincingly demonstrate that leaves with domatia have more mites; it seems plausible that leaves with more domatia should have more mites.

In summary, the evidence is clear that mite domatium association is more than coincidental. Domatia provide a sheltered microhabitat in which mites can hide, moult, and lay their eggs. The benefit which mites derive from domatia is reflected in the size of the mite population on domatium bearing leaves and in the distribution of mites on the phylloplane: Leaves with domatia have more mites than leaves without; leaves with more domatia have more mites than leaves with fewer domatia; and domatia attract more mites than domatium-less vein axils.



Fig. 18. Insect induced damage along the abaxial surface of the midrib resulted in the production of domatium-like structures on the leaf of *Olea capensis macrocarpa* (top). These structures are strikingly similar to the domatia of *Chionanthus foveolatus* (bottom).

The nature of the damage indicates that the culprits are probably caterpillars. Phytoseiid and stigmatid mites, which are the most common taxa in the domatia, are known to feed on lepidopteran eggs, and this is probably how they have their main impact (B. Burges pers. com.).

Fungivorous/epiphyll feeding mites were much less common in the domatia of *O. bullata* than predatory mites. This may explain why blocking the domatia did not affect the epiphyll populations. Epiphylls are never common enough to be visible to the naked eye, and it is possible that they do not pose much of a threat to *O. bullata*. Leaves may need to be replaced for other (physiological) reasons before epiphylls become a problem.

Paradoxically, the epiphyllous fungus *Retiarius* (both species of which are common on the leaves of *O. bullata*) might benefit the leaves on which it grows. These fungi are astonishingly effective at capturing the pollen on which they feed (Fig. 20 and 21). The capturing mechanism is so effective that the pollen is often strung along the mycelium like pearls on a necklace. Many predatory phytoseiids and stigmatids have been reported to use pollen as an alternative food source when prey is scarce (Krantz 1986). Leaves with *Retiarius* may support larger populations of predatory mites if they make use of pollen captured by the fungus.

In *C. foveolatus* there is also a lack of interaction between mites and fungus. The black leaf fungus, *Phialophora*, is the most common fungus on the leaves of *C. foveolatus*. On old leaves it may cover up to 90% of the upper leaf surface. The most common mite on the leaves of *C. foveolatus* is a species of oribatid mite (order Cryptostigmata) which accounts for 88% of the mites in domatia. The mites are almost certainly fungivorous, yet large differences (0 to 30) in the number of cryptostigmatid mites on leaves of the same rank did not affect the abundance of *Phialophora*.

O'Dowd and Willson (1989) suggest that differences in the amount of epiphylls account for the scarcity of oribatid mites on young leaves and their abundance on the old leaves of four Australian species. However, even the rank 1 leaves of *C. foveolatus*, on which

the fungus is never common, occasionally support large numbers of cryptostigmatids (Fig. 19). It is possible that the mites are feeding on less conspicuous species of fungi.

On a larger geographical scale, variation in the numbers of cryptostigmatid mites has as little effect on the abundance of *Phialophora* as local variation. At Black Slab Gully, *Phialophora* is as common as at the nearby Orange Kloof study site, however, there are no cryptostigmatid mites in the domatia of these plants. The same is true for trees growing in the Newlands forestry area. Both cryptostigmatids and *Phialophora* are absent from the Llandudno milkwood thickets (*Sideroxylon inerme*) where *C. foveolatus* is a common understory tree. It remains to be seen whether there is generally a lack of interaction between domatium inhabiting mites and fungus.

In summary: This study is the first to demonstrate that plants benefit from the activity of domatium inhabiting mites. Correlations concur with experimental results: predatory phytoseiid and stigmatid mites protect the leaves of *O. bullata* from herbivorous insects. On the other hand, the mites which inhabit the domatia of *C. foveolatus* and *O. bullata* do not appear to have an effect on epiphyllous fungi.

Ecological succession on the phylloplane

In transient environments successional changes in population size and species composition have been identified as important ecological forces (Begon *et al.* 1986). In this respect the phylloplane environment is no exception. O'Dowd and Willson (1989) found that mite occupancy varied significantly with leaf age for 9 of 12 tested species. I found that leaf rank accounted for a large proportion of the variation in the number of mites and the abundance of fungi on the leaves of *C. foveolatus* and *O. bullata*. It is obviously very important to consider the effect of leaf age in a study of mite-plant mutualism. Successional changes in the composition of the mite population will effect the quality and the type of protection offered by mites. On the other hand, as a result of successional changes in the pathogen community (fungi and herbivores), leaves may need different kinds of protection at different stages of their development.

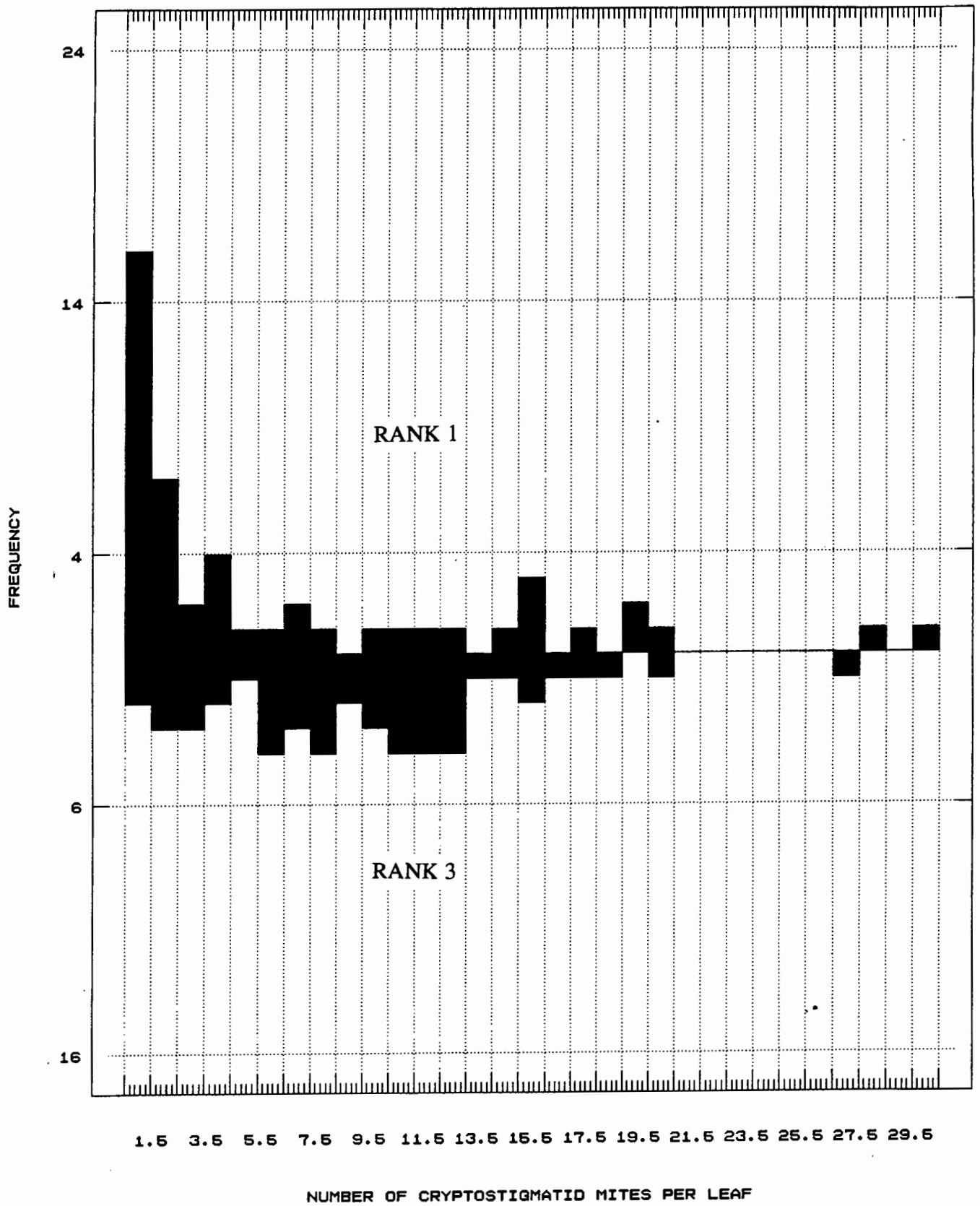


Fig. 19. Matched frequency histograms for the abundance of cryptostigmatid mites on rank 1 and rank 3 leaves of *Chionanthus foveolatus*.

Within a relatively restricted area, where soil and light conditions are more or less constant, the rate of leaf production will be similar for different individuals of the same species. Thus, within the study area leaves of the same rank will be more or less the same age and successional trends can be studied by averaging levels of occupancy for leaves of the same rank.

Time lags in population growth and colonization, and the relative abundance of food types seem to be important determinants of mite community structure. On rank 1 leaves of *C. foveolatus* cryptostigmatid mites are much less abundant than on leaves of higher rank. Another difference is that the proportion of nymphal to adult cryptostigmatids is much greater (Fig. 12). Adult cryptostigmatid mites are more active and faster moving than nymphs. Four days after introducing 13 adult cryptostigmatids to a leaf of a potted plant, 7 had moved off the leaf and were found on neighbouring leaves. In contrast, nymphs seldom venture out of the domatia. This discrepancy in the mobility of the two stages would explain the higher proportion of adult mites on young, newly colonized leaves.

The importance of colonization effects is illustrated in the frequency distributions for mite occupation on rank 1 and rank 3 leaves (Fig. 19). The only major difference between the frequency distribution for young and old leaves, is the large number of young leaves on which no, or very few mites are present. These leaves have presumably not yet been colonized, or have been colonized very recently.

Leaf age has the opposite effect on the abundance of phytoseiid and stigmatid mites on the leaves of *C. foveolatus*. Phytoseiid and stigmatid mites are significantly more abundant on rank 1 leaves, so the time lag before colonization must be short. This is to be expected since phytoseiids and stigmatids, like all hunters, are very mobile and are able to move around swiftly on their long legs. However, the greater abundance of these mites on young leaves still begs an explanation. Phytoseiids and stigmatids are known to take a wide range of food, but feed mainly on phytophagous mites, in the control of which they have been used with great success (Krantz 1986). It is possible that the predatory mites are attracted to young leaves because of the abundance of

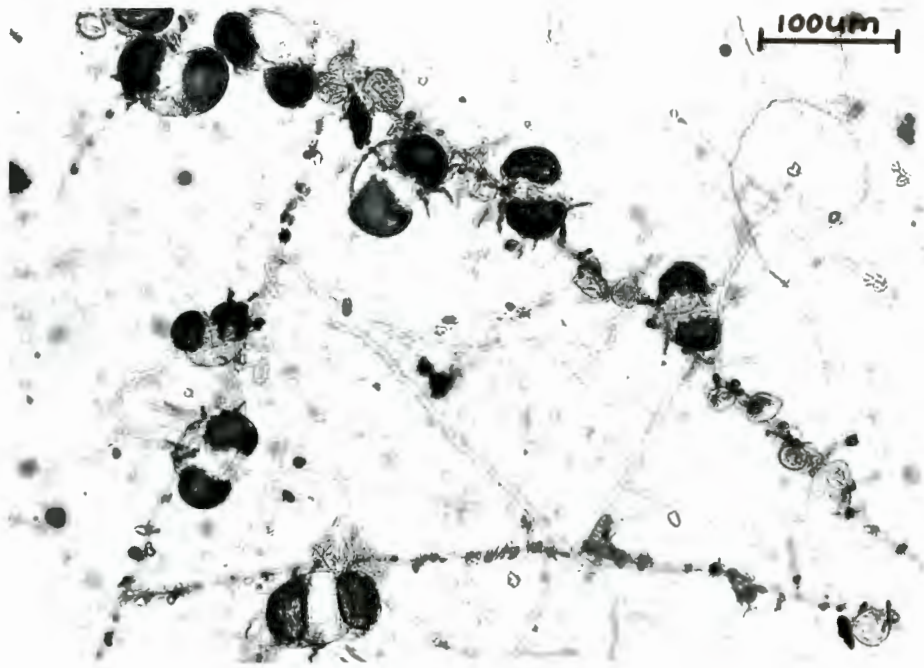


Fig. 20. Pollen from a variety of species, including gymnosperms, is trapped on the vertically projecting hyphal spikes of the pollen-capturing fungus *Retiarius superficialis* growing on *Ocotea bullata*.

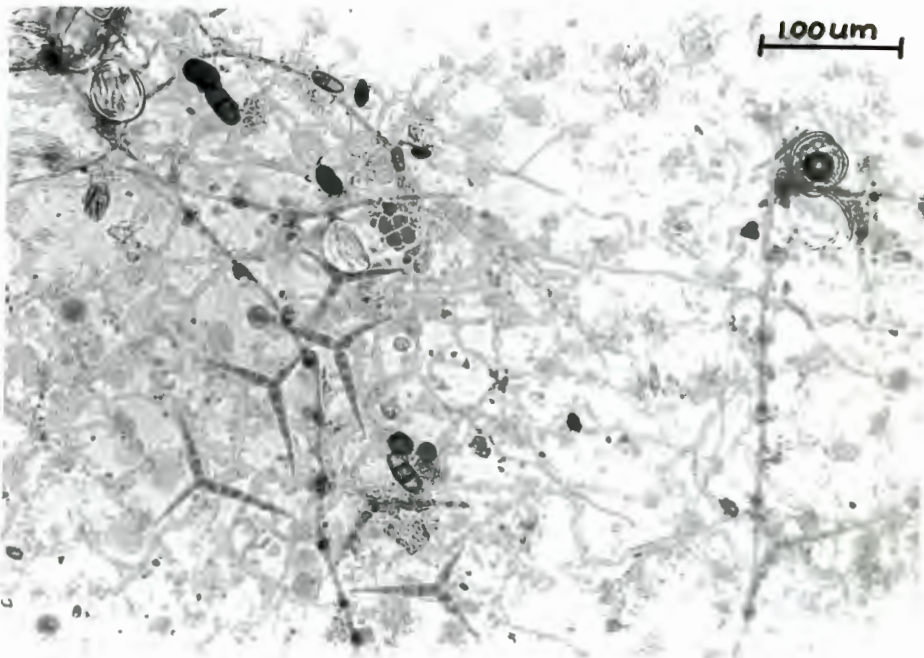


Fig. 21. The star-shaped conidia of *Retiarius superficialis* are a diagnostic feature of the species.

Mite activities which enhance the fitness of plants

It has been shown that there is a strong association between mites and domatia, and that the use of domatia enhances the fitness of mites. To prove a mutualistic relationship between mites and plants, it still needs to be shown that the activities of domatium inhabiting mites enhance the fitness of plants.

Lundstroem (1887) proposed that domatium inhabiting mites serve plants by devouring plant enemies. The trophic roles which have been tentatively been assigned to mites collected in the domatia of *O. bullata* and *C. foveolatus* lend circumstantial support to this suggestion. All the mites belong to taxa which are potentially beneficial to the plant. Fungivorous/epiphyll-feeding mites (cryptostigmatids) are the most common in the domatia of *C. foveolatus*, and predatory mites (phytoseiids and stigmatids) are the most common in the domatia of *O. bullata*.

Consistent with Lundstroem's hypothesis, *O. bullata* appears to derive benefit from the activities the domatium inhabiting, predatory mites. The leaves of *O. bullata* often suffer extensive herbivory damage. Herbivory damage takes the form of nicks along the leaf margin. The degree of damage decreases with an increase in the number of predatory mites which inhabit the domatia. Successional patterns do not explain this correlation, since neither of the variables seem to be affected by leaf age (Fig. 13 and Fig. 17).

Results from mite exclusion experiments are consistent with the correlation between predatory mites and herbivore damage, lending further support to Lundstroem's hypothesis. After 18 months the degree of herbivory damage was significantly higher to leaves with blocked domatia than to untreated leaves or leaves with mock-blocked domatia. It seems very likely that the higher incidence of herbivory in experimental leaves resulted from the reduction in the number of mites to half the number on mock-blocked leaves. The reduction in the numbers of predatory phytoseiid and stigmatid mites was probably even greater.

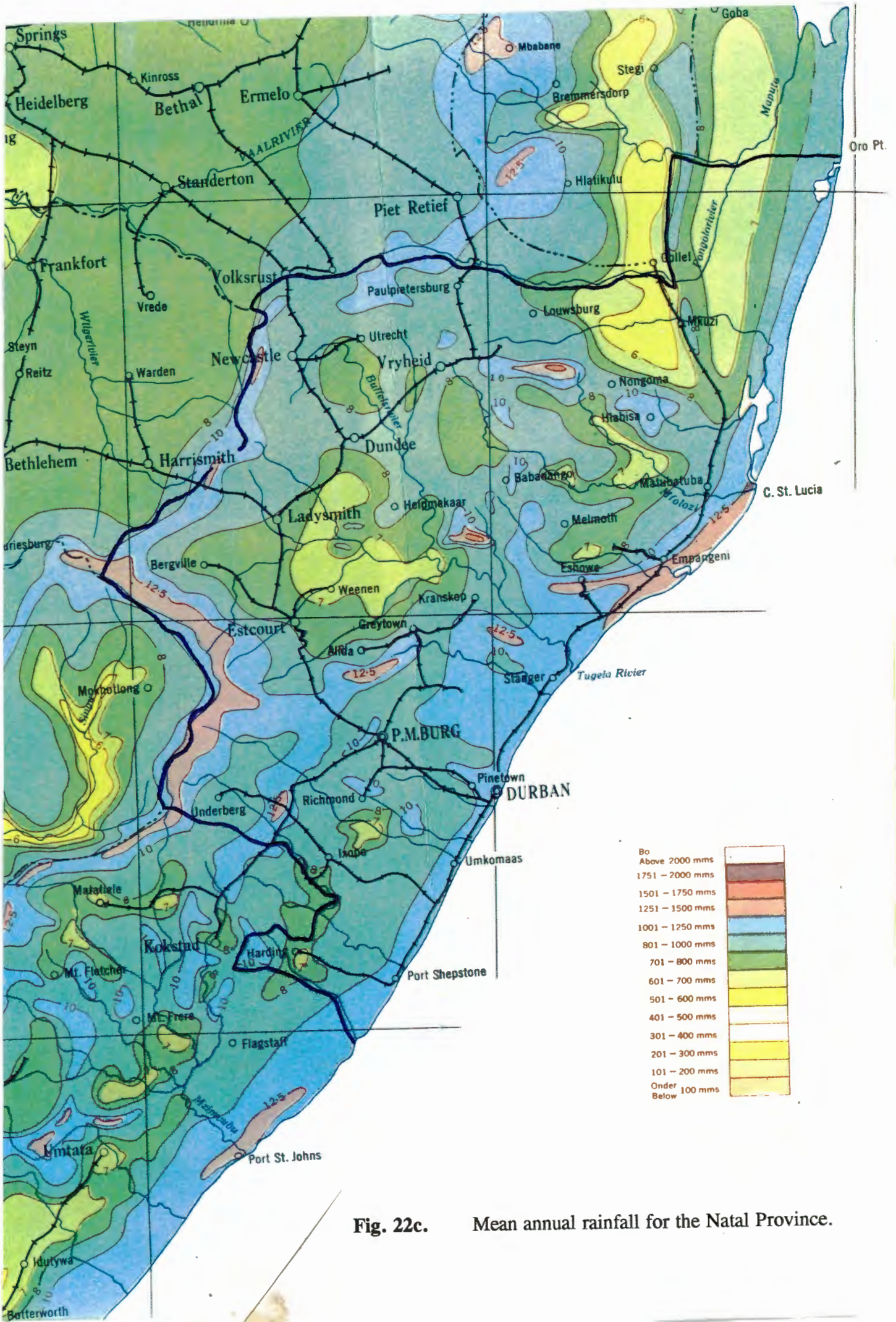


Fig. 22c. Mean annual rainfall for the Natal Province.

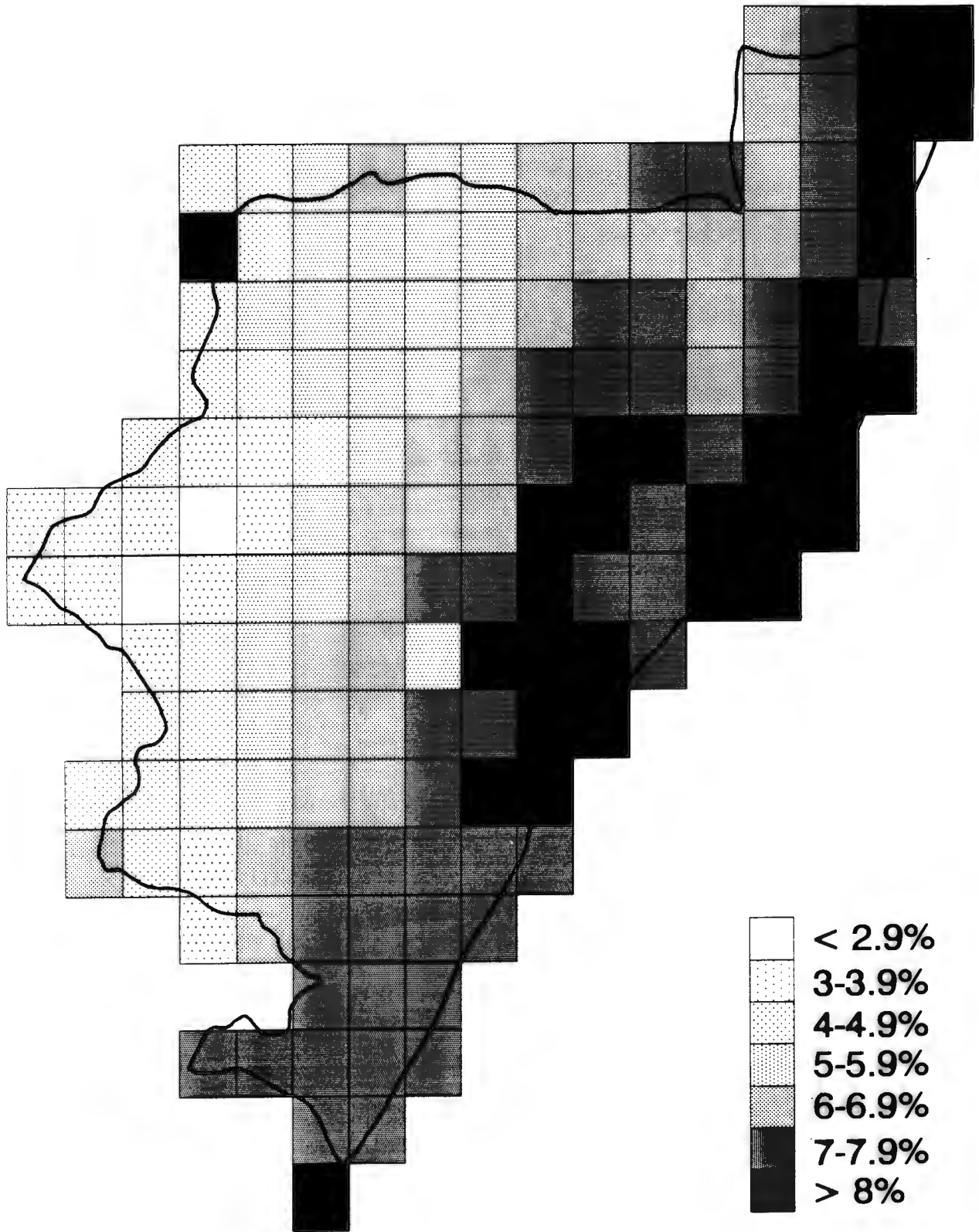


Fig. 22b.

The number of domatium bearing tree species in each quarter-degree square is expressed as a percentage of the total number of tree species occurring in the square.

phytophagous mites (Dicke and Sabelis 1988). Although there were no phytophagous mites in the domatia, they may well have been present on the leaf surface, where they usually shelter under protective silken nets.

The larger number of predatory mites on young leaves does not result from a negative interaction with oribatid mites, which are more common on the older leaves. On leaves of the same rank, the number of predatory mites generally increases as the number of cryptostigmatids increases. Thus, although the domatia of old *C. foveolatus* leaves often become clogged with the accumulating exoskeletons of oribatid mites (Fig. 4), this does not appear to limit the numbers of predatory mites on old leaves.

Although there is a great deal of fluctuation, there is no clear successional pattern in the abundance of various trophic groups on the leaves of *O. bullata* (Fig. 13). The absence of an obvious successional patterns probably means that the data which was collected was too crude to reflect changes in the abundance of different feeding groups.

Alternatively, it is possible that leaf rank is a poor measure of leaf age in the trees that were sampled.

Biogeography of domatium bearing plants

Presumably, there are more species with domatia in habitats where domatia are an advantage. Areas with many domatium bearing species may share some common environmental condition, such as poor soil. Thus, a biogeographic analysis would provide insight into the function of domatia.

I analyzed the distribution of domatium bearing trees in the Natal Province, and interpreted this pattern in relation to a number of environmental variables. The analysis showed that the fraction of tree species which bear domatia is very high near the coast, and decreases gradually and monotonically as the distance from the sea increases (Fig. 22b).

O'Dowd and Willson (1989 and 1991) suggested that domatium bearing plants are uncommon in arid areas and more plentiful where the rainfall is higher. In the areas

close to the coast, mean annual rainfall is a good predictor of the prevalence of domatium bearing species (Fig. 22c). However, along the western side of the province the sharp increase in rainfall (associated with the rise in altitude) is not accompanied by an increase in the abundance of domatium bearing species.

The humidity pattern more closely fits the biogeographic pattern. Humidity decreases gradually and monotonically with increasing distance from the coast, and the increase in rainfall along the western border of the country is not associated with an increase in humidity. Mites are very vulnerable to desiccation, and this may explain the apparent correlation between the abundance of domatium bearing species and the humidity. If there is a generally smaller arboreal mite population in the less humid areas, there will be few mites available for the plant to recruit. This hypothesis can be tested by comparing the abundance of mites in the domatia of a widespread species (e.g. *Kiggelaria africana*) from humid and less humid areas.

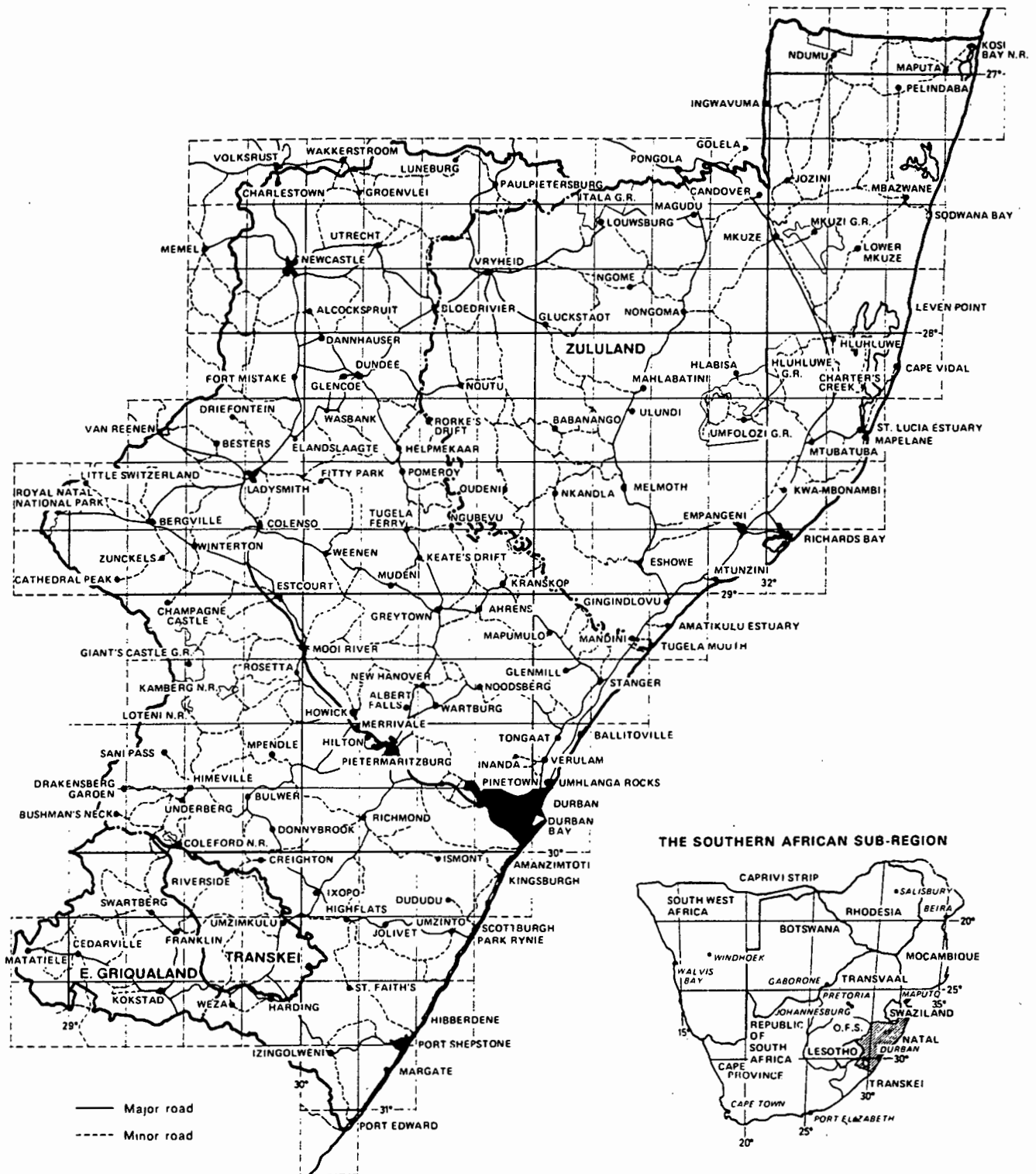


Fig. 22a. The Natal Province showing quarter-degree squares with their major place-names.

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Appendix 1. A list of the tree species used in the biogeographic analysis. A "*" designates species which were considered to have domatia.

<i>Acacia albida</i>	<i>Aloe bainesii</i>	<i>Brachylaena uniflora</i>
<i>Acacia ataxacantha</i>	<i>Aloe candelabrum</i>	<i>Brachyleana huillensis</i>
<i>Acacia borleae</i>	<i>Aloe ferox</i>	<i>Breonadia microcephala</i>
<i>Acacia brevispica</i>	<i>Aloe marlothii</i>	<i>Bridelia cathartica cathartica</i>
<i>Acacia burkei</i>	<i>Aloe puridens</i>	<i>Bridelia cathartica mlnthesoides</i>
<i>Acacia caffra</i>	<i>Aloe rupestris</i>	<i>Bridelia micrantha</i>
<i>Acacia davyi</i>	<i>Aloe sessiliflora</i>	<i>Bruguiera gymnorrhiza</i>
<i>Acacia dealbata</i>	<i>Aloe spectabilis</i>	<i>Buddleja auriculata</i>
<i>Acacia decurrens</i>	<i>Aloe thraskii</i>	<i>Buddleja dysophylla</i>
<i>Acacia gerrardii</i>	<i>Alsophila capensis</i>	<i>Buddleja loricata</i>
<i>Acacia grandicornuta</i>	<i>Alsophila dregei</i>	<i>Buddleja pulchella</i>
<i>Acacia karoo</i>	<i>Amphloia theiformis</i>	<i>Buddleja saligna</i>
<i>Acacia kraussiana</i>	<i>Anastrabe integerrima</i>	<i>Buddleja salviifolia</i>
<i>Acacia longifolia</i>	<i>Ancylanthos monteiroi</i>	<i>Burchellia bubalina</i>
<i>Acacia luederitzii</i>	<i>Andrachne ovalis</i>	<i>Buxus natalensis</i>
<i>Acacia mearnsii</i>	<i>Androstachys johnsonii</i>	<i>Cadaba natalensis</i>
<i>Acacia melananoxydon</i>	<i>Annona senegalensis</i>	<i>Caesalpinia bonduc</i>
<i>Acacia nigrescens</i>	<i>Antidesma venosum</i>	<i>Caesalpinia decapetala</i>
<i>Acacia nilotica</i>	<i>Apodytes dimidiata</i>	<i>Calodendrum capense</i>
<i>Acacia podalyrifolia</i>	<i>Artabotrys monteiroae</i>	<i>Calpurnia aurea</i>
<i>Acacia robusta robusta</i>	<i>Atalaya alata</i>	<i>Calpurnia intrusa</i>
<i>Acacia robusta clavigera</i>	<i>Avicennia marina</i>	<i>Calypha sonderana</i>
<i>Acacia schweinfurthii</i>	<i>Azima tetracantha</i>	* <i>Canthium ciliatum</i>
<i>Acacia senegal</i>	<i>Bachmannia woodii</i>	* <i>Canthium gueinzii</i>
<i>Acacia sieberana</i>	<i>Balanites maughamii</i>	* <i>Canthium inerme</i>
<i>Acacia swazica</i>	<i>Balanites pedicellaris</i>	* <i>Canthium locuples</i>
<i>Acacia tortilis</i>	<i>Baphia racemosa</i>	<i>Canthium mundianum</i>
<i>Acacia xanthophloea</i>	<i>Barringtonia racemosa</i>	* <i>Canthium pauciflorum</i>
<i>Acalypha glabrata</i>	<i>Bauhinia bowkeri</i>	* <i>Canthium setiflorum</i>
<i>Acokanthera oblongifolia</i>	<i>Bauhinia galpinii</i>	* <i>Canthium spinosum</i>
<i>Acokanthera oppositifolia</i>	<i>Bauhinia natalensis</i>	<i>Capparis sepiaria</i>
<i>Acokanthera schimperii</i>	<i>Bauhinia tomentosa</i>	<i>Capparis tomentosa</i>
<i>Acridocarpus natalitius</i>	<i>Beilschmiedia natalensis</i>	<i>Carissa bispinosa</i>
<i>Adenia gummifera</i>	<i>Bequaertiodendron natalense</i>	<i>Carissa macrocarpa</i>
<i>Afzelia quanzensis</i>	<i>Bequaertiodendron magalismontanum</i>	<i>Carissa tetramera</i>
<i>Alberta magna</i>	<i>Berchemia discolor</i>	<i>Carissa wyliei</i>
<i>Albizia adianthifolia</i>	<i>Berchemia zeyheri</i>	<i>Casearia gladiiformis</i>
<i>Albizia anthelmintica</i>	<i>Bersama lucens</i>	<i>Cassia didymobotrya</i>
<i>Albizia forbesii</i>	<i>Bersama swinnyi</i>	<i>Cassia florabunda</i>
<i>Albizia lebbeck</i>	<i>Bersama tysoniana</i>	<i>Cassia petersiana</i>
<i>Albizia petersiana</i>	* <i>Blighia unijugata</i>	<i>Cassine aethiopica</i>
<i>Albizia suluensis</i>	<i>Bolusanthus speciosus</i>	<i>Cassine crocea</i>
<i>Albizia versicolor</i>	<i>Boscia albitrunca</i>	<i>Cassine eucleiformis</i>
<i>Alchornea hirtella</i>	<i>Boscia foetida</i>	<i>Cassine papillosa</i>
<i>Allocassine laurifolia</i>	<i>Bowkeria citrina</i>	<i>Cassine peragua</i>
<i>Allophylus africanus</i>	<i>Bowkeria verticillata</i>	<i>Cassine tetragona</i>
* <i>Allophylus decipiens</i>	<i>Brachylaena discolor</i>	<i>Cassine transvaalensis</i>
* <i>Allophylus dregeanus</i>	<i>Brachylaena elliptica</i>	<i>Cassine velutinum</i>
<i>Allophylus natalensis</i>	<i>Brachylaena glabra</i>	<i>Cassinopsis ilicifolia</i>
<i>Aloe arborescens</i>	<i>Brachylaena ilicifolia</i>	<i>Cassinopsis tinifolia</i>

Cassipourea gerrardii	Cryptocarya myrtifolia	Entada pursaetha
Cassipourea gummiflora	Cryptocarya latifolia	Entada spicata
Cassipourea mossabicensis	Cryptocarya wyliei	Entandophragma caudatum
Casuarina equisetifolia	Cunonia capensis	Enterospermum littorale
Catha edulis	Curtisia dentata	Ephippiocarpa orientalis
Cavacoa aurea	Cussonia arenicola	Erica caffra
Ceiba pentandra	Cussonia natalensis	Erica caffrorum
Celtis africana	Cussonia nicholsonii	Erithroxylum pictum
Celtis gomomorphylla	Cussonia paniculata	Erythrina caffra
Celtis milbraedii	Cussonia sphaerocephala	Erythrina humeana
* Cephalanthus natalensis	Cussonia spicata	Erythrina latissima
Ceriops tagal	Cussonia zuluensis	Erythrina lysistemom
Cestrum laevigatum	Dais cotinifolia	Erythrococca berberidea
Chaetacme aristata	Dalbergia armata	Erythrophleum lasianthum
Choristylis rhamnoides	Dalbergia multijuga	Erythroxylum delagoense
Chrisantemoides monilifera	Dalbergia nitidula	Euclea crispa
Chrysophyllum viridifolium	Dalbergia obovata	Euclea divinatorum
Cladostemon kirkii	Deinbollia oblongifolia	Euclea natalensis
Clausena anisata	* Dialium schlechteri	Euclea schimperi
Cleistanthus schlechteri	Dichrosthachys cinerea	Euclea undulata
Clerodendrum glabrum	Dinocanthium hystrix	Eugenia capensis capensis
Clerodendrum myricoides	Diospyros austro-africana	Eugenia capensis natalitia
Cliffortia nitidula	Diospyros dichrophylla	Eugenia capensis zeyheri
Clusia abyssinica	Diospyros glandulifera	Eugenia erythrophylla
Cnestis natalensis	Diospyros inhacaensis	Eupatorium odoratum
Coffea racemosa	Diospyros natalensis	Euphorbia cooperi
Cola greenwayi	Diospyros rotundifolia	Euphorbia evansii
Cola natalensis	Diospyros scabrida	Euphorbia grandidens
Colpoon compressum	Diospyros simii	Euphorbia ingens
Combretum apiculatum	Diospyros villosa	Euphorbia tetragona
Combretum bracteosum	Diospyros whyteana	Euphorbia tirucalli
Combretum celastroides	Dombeya burgessiae	Euphorbia triangularis
Combretum collinum	Dombeya cymosa	Faurea manaughtonii
Combretum edwardsii	Dombeya rotundiflora	Faurea saligna
Combretum erythrophyllum	Dombeya tiliacea	Faurea speciosa
Combretum hereroense	Dovyalis caffra	Ficus bizanae
Combretum imberbe	Dovyalis longispina	Ficus burtt-davyi
* Combretum kraussii	Dovyalis lucida	Ficus capensis
Combretum molle	Dovyalis rhamnoides	Ficus capreifolia
Combretum paniculatum	Dovyalis zeyheri	Ficus craterostoma
Combretum xanthoxyrisum	Dracaena hookerana	Ficus ingens
* Combretum zeyheri	Dracaena usambarensis	Ficus natalensis
Commiphora harveyi	Drypetes arguta	Ficus petersii
Commiphora neglecta	Drypetes gerrardii	Ficus polita
Commiphora pyracanthoides	Drypetes natalensis	Ficus salicifolia
Commiphora schimperi	Duvernoia adhatodoides	Ficus sansibarica
Commiphora woodii	Dyospyros lycioides	Ficus soldanella
Commiphora zanzibarica	* Eheretia rigida	Ficus sonderi
Cordia caffra	Ehretia amoena	Ficus stuhlmannii
Cordia ovalis	Ekebergia capensis	Ficus sycomorus
Cordyla africana	Ekebergia pterophylla	Ficus tremula
Craibia zimmermannii	Embelia ruminata	Ficus trichopoda
Crassula ovata	Encephalartos altensteinii	Ficus verruculosa
Crotalaria capensis	Encephalartos ferox	Ficus vogelii
Croton gratissimus	Encephalartos ghellinckii	Galpinia transvaalica
Croton menyhartii	Encephalartos lebomboensis	Garcinia gerrardi
Croton pseudopulchellus	Encephalartos natalensis	Garcinia livingstonei
Croton steenkampianus	Encephalartos woodii	Gardenia amoena
Croton sylvaticus	Endata wahlbergii	* Gardenia spatulifolia
Cryptocarya woodii	Englerodaphne pilosa	* Gardenia thunbergii

Gerrardina foliosa	Maerua angolensis	Olinia ventosa
Grewia bicolor	Maerua cafra	Oncinotis inandensis
Grewia caffra	Maerua nervosa	Oncoba spinosa
Grewia flava	Maerua racemulosa	Opuntia spp
Grewia flavescens	Maerua rosmarinoides	Oricia bachmannii
Grewia gracillina	Maesa alnifolia	Ormocarpum trichocarpum
Grewia hexamita	Maesa lanceolata	Osyris lanceolata
Grewia hispida	Magnifera indica	Oxanthus latifolius
Grewia lasiocarpa	Manilkara concolor	Oxanthus pyriformis
* Grewia microthyrsa	Manilkara discolor	* Oxanthus gerrardi
Grewia monticola	Manilkara mochisia	Ozoroa engeleri
Grewia occidentalis	Maytenus acuminata	Ozoroa obovata
Grewia subspathulata	Maytenus bachmanii	Ozoroa paniculosa
Grewia villosa	Maytenus hetophyll	Pachystigma macrocalyx
Greyia radlkoferi	Maytenus mossambicensis	Pancovia golungensis
Greyia sutherlandii	Maytenus nemorosa	Pappea capensis
Guettarda speciosa	Maytenus penduncularis	Parinari curatellifolia
Hakea tenuifolia	Maytenus procumbens	Passerina filiformis
Halleria lucida	Maytenus senegalensis	Passerina montana
Haplocoelum gallense	Maytenus undata	Passerina rigida
Harpephyllum caffrum	Melia azedarach	* Pavetta alexandrae
Heteromorpha arborescens	Memecylon natalense	Pavetta assimilis
* Heteropyxis natalensis	Memecylon sansibaricum	* Pavetta bowkeri
Heywoodia lucens	Micrococca capensis	* Pavetta catophylla
Hibiscus tiliaceus	Millettia grandis	* Pavetta cooperi
Hippobromus pauciflorus	Millettia sutherlandii	Pavetta edentula
Hippocratea africana	Mimusops caffra	* Pavetta galpinii
Hippocratea delagoensis	Mimusops obovata	Pavetta gerstneri
Holmskioldia tettensis	Mimusops zeyheri	* Pavetta natalensis
Homalium dentatum	Monanthes caffra	* Pavetta revoluta
Homalium rufescens	Monodora sunodii	Pavetta schumanniana
Hymenocardia ulmoides	Montanoa bipinnatifida	Peddiea africana
Hyphaene natalensis	Montanoa hibiscifolia	Peddiea fischeri
Iboza riparia	Morus mesozygia	Peltophorum africanum
Ilex mitis	Mundulea sericea	Pereskia aculeata
Indigofera cylindrica	Myrica pilulifera	Phillipia evansii
Indigofera natalensis	Myrica serrata	Phoenix reclinata
Jacaranda mimosifolia	Myrsine africana	Phylla paniculata
Kigelia africana	Myrsine pillansii	Phyllanthus cedrelifolius
* Kiggelaria africana	Nectaropetalum capense	Phyllanthus discoideus
* Kraussia floribunda	Nectaropetalum zuluense	Phyllanthus reticulatus
Lagynias lasiantha	Newtonia hildebrandtii	Phyllanthus sp
Landolphia kirkii	Nhambanella henriquesii	Piper capensis
Landolphia petersiana	Nuxia congesta	Pisonia aculeata
Lansea discolor	Nuxia floribunda	Pittosporum viridiflorum
Lansea stuhlmannii	Nuxia opositifolia	Plectroniella armata
Lantana camara	Ochna arborea	Pleurostyliia capensis
Lasiodiscus mildbraedii	Ochna holstii	Podocarpus falcatus
Leucaena leucocephala	Ochna inermis	Podocarpus henkelii
Leucosidea sericea	Ochna natilitia	Podocarpus latifolius
* Linociera foveolata	Ochna serrulata	Polygala myrtifolia
* Linociera peglerae	* Ocotea bullata	Portulacaria afra
Lippia javanica	Ocotea kenyensis	Pouzolzia hypoleuca
Litsea sebifera	Odonaea viscosa	Premna mooiensis
Lonchocarpus capassa	Olax dissitiflora	Protea gaguedi
Lopholaena platyphylla	Olea africana	Protea multibracteata
Loxostylis alata	Olea capensis	Protea roupelliae
Lumnitzera racemosa	Olea capensis enervis	Protea subvestita
Lycium acutifolium	Olea woodiana	Protea welwitschii
Macaranga capensis	Olinia emarginata	Protorhus longifolia
* Mackaya bella	Olinia radiata	Prunus africana

<i>Pseudobersama mossambicensis</i>	<i>Schefflera umbelifera</i>	<i>Trichocladus grandiflorus</i>
<i>Pseudosalacia streyi</i>	<i>Schotia brachypetala</i>	<i>Trimeria grandifolia</i>
<i>Pseudoscolopia polyantha</i>	<i>Schotia capitata</i>	* <i>Trimeria trinervis</i>
<i>Psidium cattleianum</i>	<i>Schotia sp</i>	<i>Turraea obtusifolia</i>
<i>Psidium guajava</i>	<i>Schrebera alata</i>	<i>Turraea floribunda</i>
<i>Psoralea pinnata</i>	<i>Sclerocarya caffra</i>	<i>Urera cameroonensis</i>
* <i>Psychotria capensis</i>	<i>Scolopia flanagannii</i>	<i>Urera tenax</i>
<i>Pfaeroxylon obliquum</i>	<i>Scolopia mundii</i>	<i>Uvaria caffra</i>
<i>Pteleopsis myrtifolia</i>	<i>Scolopia oreophila</i>	<i>Uvaria lucida</i>
<i>Pterocarpus angolensis</i>	<i>Scolopia stoltzii</i>	<i>Vaccinium exul</i>
<i>Pterocarpus rotundifolius</i>	<i>Scolopia zeyheri</i>	<i>Vangueria esculenta</i>
<i>Pterocelastrus echinatus</i>	<i>Securinea virosa</i>	<i>Vangueria infusta</i>
<i>Pterocelastrus rostratus</i>	<i>Seemannaralia gerrardii</i>	<i>Vepris carringtoniana</i>
<i>Putterlickia sp.</i>	<i>Sesbania punicea</i>	<i>Vepris lanceolata</i>
<i>Putterlickia verrucosa</i>	<i>Sesbania sesban</i>	<i>Vepris reflexa</i>
<i>Putterlinkia sp</i>	<i>Sideroxylon inerme</i>	<i>Veronia colorata</i>
<i>Quisqualis parviflora</i>	<i>Smodingium argutum</i>	<i>Vitellariops dispar</i>
<i>Rapaena melanophloes</i>	<i>Solanum aculeastrum</i>	<i>Vitellariopsis marginata</i>
<i>Raphia australis</i>	<i>Solanum giganteum</i>	<i>Vitex amboniensis</i>
<i>Rauvolfia caffra</i>	<i>Solanum mauritianum</i>	* <i>Vitex harveyana</i>
<i>Rawsonia lucida</i>	<i>Sophora inhambanensis</i>	<i>Vitex obovata</i>
<i>Rhamnus prinoides</i>	<i>Spirostachys africana</i>	<i>Vitex rehmannii</i>
<i>Rhibozum Zambesiacum</i>	<i>Sterculia rogersii</i>	<i>Vitex wilmsii</i>
<i>Rhizophora mucronata</i>	<i>Strelitzia nicolai</i>	<i>Voacanga thouarsii</i>
<i>Rhoicissus digitata</i>	<i>Strophanthus speciosus</i>	<i>Warburgia salutaris</i>
<i>Rhoicissus reviolii</i>	<i>Strychnos decussata</i>	<i>Widdringtonia nodiflora</i>
<i>Rhoicissus rhomboidea</i>	<i>Strychnos henningsii</i>	<i>Wrightia natalensis</i>
<i>Rhoicissus tomentosa</i>	<i>Strychnos madagascariensis</i>	<i>Xeromphis obovata</i>
<i>Rhoicissus tridentata</i>	<i>Strychnos sp</i>	* <i>Xeromphis rudis</i>
<i>Rhus chirindensis</i>	<i>Strychnos spinosa</i>	<i>Ximenia americana</i>
<i>Rhus dentata</i>	<i>Strychnos usambarensis</i>	<i>Ximenia caffra</i>
<i>Rhus dura</i>	<i>Suregada africana</i>	<i>Xylothea kraussiana</i>
<i>Rhus fastigiata</i>	<i>Suregada procera</i>	<i>Xymalos monospora</i>
<i>Rhus fraseri</i>	<i>Suregada zanzibariensis</i>	<i>Yucca sp</i>
<i>Rhus gueinzii</i>	<i>Synadenium cupulare</i>	<i>Zanthoxylem capense</i>
<i>Rhus lucida</i>	<i>Synaptolepis kirkii</i>	<i>Zanthoxylem davyi</i>
<i>Rhus macowanii</i>	<i>Syzygium cordatum</i>	<i>Zanthoxylem lepreurii</i>
<i>Rhus montana</i>	<i>Syzygium guineense</i>	<i>Ziziphus mucronata</i>
<i>Rhus natalensis</i>	<i>Tabernaemontana elegans</i>	<i>Ziziphus rivularis</i>
<i>Rhus nebulosa</i>	<i>Tabernaemontana ventricosa</i>	
<i>Rhus pentheri</i>	* <i>Tapura fischeri</i>	
<i>Rhus pyroides</i>	<i>Tarchonanthus camphoratus</i>	
<i>Rhus rehmanniana</i>	<i>Tarchonanthus trilobus</i>	
<i>Rhus tomentosa</i>	* <i>Tarenna junodii</i>	
<i>Rhus transvaalensis</i>	<i>Tarenna neurophylla</i>	
<i>Rhus undulata</i>	* <i>Tarenna pavettoides</i>	
<i>Rhynchocalyx lawsonoides</i>	<i>Teclea gerrardii</i>	
<i>Ricinus communis</i>	<i>Teclea natalensis</i>	
<i>Rinorea angustifolia</i>	<i>Terminalia phanerophlebia</i>	
<i>Rinorea ilicifolia</i>	<i>Terminalia sericea</i>	
* <i>Rothmannia capensis</i>	<i>Thespesia acutibola</i>	
* <i>Rothmannia fischeri</i>	<i>Thilachium africanum</i>	
* <i>Rothmannia globosa</i>	<i>Toddaliopsis bremkampii</i>	
<i>Ruttya ovata</i>	<i>Trema orientalis</i>	
<i>Salacia gerrardi</i>	* <i>Tricalysia capensis</i>	
<i>Salacia leptoclada</i>	<i>Tricalysia lanceolata</i>	
<i>Salix babylonica</i>	<i>Tricalysia sonderana</i>	
<i>Salix subserrata</i>	<i>Trichilia dregeana</i>	
<i>Salvadora angustifolia</i>	<i>Trichilia emetica</i>	
<i>Sapium ellipticum</i>	<i>Trichocladus crinitus</i>	
<i>Sapium integerrimum</i>	<i>Trichocladus ellipticus</i>	

Appendix 2

Mite taxa identified from the domatia of *O. bullata*.

Predators:

Stigmaeidae 1) *Agistemus africanus* Meyer & Ryke
2) *Mulleteria neomaculata* Meyer & Ryke

Phytoseiidae 1) *Amblyseius addoensis* Van der Merwe & Ryke

Cunaxidae 1) *Rubroscirus cf. vestus* Den Heyer

Epiphyll feeders:

Tydeidae 1) *Tydeus fustis* Ueckermann
2) *Tydeus* sp. 1
3) *Triophtydeus myacanthus* Meyer & Ueckermann

Oribatei 1) one unidentified species

Arthropod parasites:

Pyemotidae 1) *Pyemotes* sp.

Unknown feeding habits:

Eupodidae 1) *Eupodes* sp.