

Do tenants always pay their rent? The Asian ant-plant *Pometia pinnata* (Sapindaceae) and its leaf domatia provide free access to generalist ants

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Abstract. The tree *Pometia pinnata* Forst. forma *glabra* (Bl.) Jacobs is an ant-plant that provides lodging (leaf domatia) and food (extrafloral nectar, excretions of coccids) for ants. The leaf domatia are formed by two pairs of strongly modified basal leaflets. In total, 63 ant species from 18 genera and 4 subfamilies were encountered in the domatia of the host in the study area (Ulu Gombak, Malaysia). We found that the ant/*Pometia* relationship has two stages: (i) an early 'myrmecophilic' phase of juvenile, domatia-free plants, and (ii) a 'myrmecophytic' phase of older plants in which ants nest in domatia. In the myrmecophilic stage, our short-term experiment revealed a significant greater loss of young leaflets when ants were excluded than on control plants to which ants had access; however, the area of remaining leaf was not different between treatment and control. Similar ambiguous effects were observed in the myrmecophytic stage: a snapshot census revealed no significant difference in the standing level of leaf herbivore damage between branches with and without nesting ants. However, our survey indicated that ant species differed in the protection provided to their host. Our data also suggest that presence of nesting ants substantially reduces damage to the leaf rachis.

Keywords: ant-plant interaction, protection mutualism, conditional outcome, leaf domatia, myrmecophyte, *Pometia*, *Lepisanthes*, Malaysia, SE Asia

INTRODUCTION

Mymecophytes, or ant-plants, offer preformed nesting space to ants in the form of domatia and also frequently furnish food, either directly (in the form of food bodies and/or extrafloral nectar) or indirectly (excretions of trophobiotic hemipterans). While some myrmecophytes form highly specific partnerships in which specialised plant-ants protect their host plants against herbivory, fungal pathogens, encroaching vines, and sometimes neighbouring vegetation (see reviews, Davidson & McKey 1993; Heil & McKey 2003), others offer their domatia to a variety of opportunistically nesting ants (e.g., Maschwitz *et al.* 1994; Alonso

1998; Djieto-Lordon *et al.* 2004) and the protective efficacy of these ants is often less pronounced.

In all ant/plant mutualisms the degree of protection can vary among ants but facultative associations involving opportunistic ants are often characterised by a particularly high variation in anti-herbivore protection (e.g., Oliveira *et al.* 1999; Di Giusto *et al.* 2001; Hossaert-McKey *et al.* 2001; Bizerril & Vieira 2002; Moog *et al.* 2002). In such associations, the ant-housing structures and/or food resources are usually open to a broad range of ant taxa resulting in high spatial and temporal variability in the outcome of the ant/plant relationship. It has been argued that the presence of ant-housing structures (or other resources)

open to invasion by numerous nonspecialist ants limits strong pairwise co-evolutionary interactions because it does not produce predictable associations between pairs of species (Moog *et al.* 2002; Djieto-Lordon *et al.* 2005).

In the last two decades a great number of formerly unknown myrmecophytes with a high diversity of ant-housing structures have been discovered in the rainforests of Southeast Asia (reviewed in Moog *et al.* 2003).

In Southeast Asia, the prevalent type of domatia in facultative associations are stem hollows to which ants gain access via self-opening, splitting stems or the activity of stem-boring insects, and leaf domatia are comparatively rare (Moog *et al.* 2003). Here we present a new association, involving a plant that offers peculiar pseudostipular domatia, composed of reflexed basal leaflets: the Sapindaceae tree *Pometia pinnata*, known as “kasai” in Malay. In this study, we ask the following questions: (1) What resources are provided for ants and when are they produced during plant ontogeny? (2) What proportion of domatia and domatia-bearing trees support ants? (3) Which ant species occupy *P. pinnata* trees? and (4) Do the ants protect their host?

Similarly-composed pseudostipular leaf domatia were also found in species of the sapindacean genus *Lepisanthes*, and we present some preliminary observations on the relationship with ants.

MATERIALS AND METHODS

Study site

The study was conducted on a population of *Pometia pinnata* located along the Gombak River in a secondary forest about 40 km northeast of Kuala Lumpur in the Ulu Gombak valley (3°19'N, 101°45'E, 250–400 m a.s.l.), West Malaysia, between January and July 1999. The area is characterised by a perhumid tropical climate with no pronounced dry season and little seasonal variation in temperature.

Species studied

The tree *Pometia pinnata* J.R. Forst. & G. Forst. (Sapindaceae) is a variable species. Jacobs (1962)

gave an extensive treatment of the species into eight forms. Adema *et al.* (1994), however, did not follow Jacobs' subdivision because they found an important portion of the material to be intermediate between two or more forms. Jacobs (1962), however, was aware of the difficulties of covering the whole variability of *P. pinnata* by distinguishing infraspecific taxa and he discussed this problem in some depth (pp. 109–113). At present, we feel justified in treating the domatia-bearing trees of *P. pinnata* as *P. p.* forma *glabra* (Bl.) Jacobs because no other Malayan forms bear domatia.

Pometia pinnata forma *glabra* is a buttressed tall tree growing up to 40 m, or rarely 50 m, in height. The leaf rachis may be 1 m long, with up to 13 leaflets on either side. Leaflets are coriaceous and to 4 mm-stalked. Their midrib and nerves are always glabrous above. *Pometia p.* forma *glabra* is distributed throughout the perhumid Sunda and Sahul shelf, reaching westward to the Nicobars, Andamans and Sri Lanka and eastward to New Guinea and New Britain (Jacobs 1962).

The tree grows in primary and secondary lowland and hill forest along creeks and streams. It is even planted at road sides and in parks because of its spectacular shiny reddish bunches of new leaves.

Early during the study it became apparent that extrafloral nectaries (EFNs) developed much earlier during plant ontogeny than leaf domatia. In younger plants, still devoid of domatia, the EFNs attracted visiting ants from the surroundings. Older plants also produced EFNs but provided another ant reward, the leaf domatia. These two stages of the ant/*Pometia* relationship are reflected in our experimental set-ups.

Development of leaves, domatia, and activity of foliar nectaries

One flush (new leaf) per tree was selected, and the development of each leaflet, the appearance of EFNs, the period of their activity, and the presence of ants at the EFNs were monitored weekly over a period of three months. A total of 28 individual trees from two size classes were included (18 trees ranging in height from 0.25 to 2.0 m and 10 trees ranging in height from 6.0 to 8.5 m).

Fauna of leaf domatia and occupation frequency

An additional 79 domatia-bearing plants (2 to 30 m high) were checked for ant and other invertebrate inhabitants. Larger trees, up to 30 m in height, had to be climbed, and 2 to 4 branches per tree were collected for immediate examination. A few individuals of each ant species were collected and preserved in 75% ethanol, then identified to genus and morpho-species level where possible. The presence of brood, alates and trophobiotic scale insects was recorded. The proportion of leaf domatia per tree occupied by ants was censused in 45 trees (3.0–15 m tall). Voucher specimens of the ants were deposited at the Senckenberg Museum in Frankfurt am Main, Germany.

Ant activity

In order to test if ant presence on a plant is influenced by the distribution of active EFNs, ant presence was counted hourly during two 24-h cycles on the following three parts of six domatia-free treelets: the trunk (40 cm long section); one mature leaf with no or few active EFNs; and one young leaf with abundant active EFNs. The median number of ants per hour on a given plant part was used for statistical comparison (Friedman test; StatView 4.51, Abacus Concepts, Inc., Berkeley, California, USA).

Plant protection by ants

To evaluate the influence of ants on leaf damage of *P. pinnata* we conducted a series of experiments which included both stages of the ant/*Pometia* relationship. First, for the myrmecophilic phase, level of herbivore damage to young developing leaves, with active EFNs, of juvenile domatia-free plants was compared between (a) plants to which visiting ants had access to EFNs (controls) and (b) those to which ants were excluded using tangle traps (experimentals). The experiment was conducted on 51 neighbouring plants (0.24–2.1 m in height) with young developing leaves (35 leaves from 26 experimental plants and 37 leaves from 25 controls). After four weeks we scored the level of herbivory by drawing the remaining leaf contour onto graph paper. After reconstructing the original

entire leaf outline, herbivore damage was expressed as percentage of the missing leaf area. (After four weeks all leaves still produced extrafloral nectar.) As a conservative measure, missing leaflets were not taken into account in assessing extent of herbivory but the number of missing leaflets was scored and analysed separately.

For the mature, myrmecophytic phase, featuring domatia-bearing trees with established ant colonies, a snapshot method was applied. Because ant-inhabited branches of the large domatia-bearing trees were not accessible for experimental manipulation (e.g., applying a tangle trap at the branch apices to exclude ants, and regularly checking the exclusion barrier for integrity), we cut down branches whose domatia were occupied by nesting ants and compared the present amount of leaf herbivory damage (standing level) with that of domatia-free juvenile plants to which visiting ants had free access. The leaves selected for comparison between domatia-free and nearby domatia-bearing plants were of similar age and included young to recently-matured leaves. Scoring for leaf damage was carried out by visually assigning each leaflet – except the two basal pairs which are involved in the domatium – to one of four defoliation levels: 1 (0–10%), 2 (11–25%), 3 (26–50%), and 4 (>50%). In total, we assessed leaf area loss from 3743 leaflets of 6 large domatia-bearing trees (>18 m in height) and from 518 leaflets of 18 domatia-free plants (1.8–3.6 m). Because we selected domatia-bearing trees occupied by established colonies of different ant species, we were able to analyse leaf herbivory for each ant species separately. Data on leaf area losses were analysed using the non-parametric Mann-Whitney U-test (two-tailed; StatView 4.51).

To examine the relationship between density of occupation of trees by ants and the presence of leaf rachis damage by stem borers, we compared the percentage of leaves bearing rachis holes between trees whose branches were ‘strongly’ ($n = 21$ trees) or ‘weakly’ ($n = 12$) colonised (> 75% and < 25% of all branches per tree colonised, respectively). Tree height ranged from 4.5 to 20 m but did not differ significantly between the two categories (U-test, $n_{strongly} = 21$, $n_{weakly} = 12$, $U = 77.5$, $P = 0.07$, n.s.).

Pseudostipules in *Lepisanthes*

In another genus of the Sapindaceae, *Lepisanthes*, pseudostipules have been described in eight species, among which the use of these structures as ant shelters has, to our knowledge, been mentioned only for *L. amoena* (Hassk.) Leenh. (Adema *et al.* 1994) and *L. alata* (Bl.) Leenh., (Schimper 1898: cited as *Capura alata* (Bl.) Teijsm. & Binn.). In the Ulu Gombak valley we encountered four trees of *L. amoena*, 3–6 m in height. These trees were examined for the presence of EFNs, pseudostipules and ant inhabitants.

RESULTS

Leaf development and extrafloral nectaries

On average, leaflets reached their final size after about six weeks but the basal leaflets (which form the domatia) began their growth first; successive leaflets followed along the leaf rachis until the distal leaflets ended their growth, in the 12th week at the latest. For about three weeks the young leaves remained bright red or pink. Each individual tree produced leaf bunches continuously throughout the year.

During their development all leaflets possessed glands which produced nectar. The EFNs are small bowl-like structures on the

underside or edge of the leaflets. They were bright green or red during their active phase, then becoming dull brownish. The largest nectaries, more than 1 mm in diameter, appeared first. They were located at the base of the leaflets close to the midrib. Smaller nectaries were found along both sides of the midrib, whereas the smallest nectar glands were located at the margins of the leaflets close to the indentation tips.

In the basal pair of leaflets, EFNs were active for about nine weeks whereas those of the distal pair developed later but remained active for 12 to 14 weeks because dried glands were continuously replaced by new ones at other sites of the leaflet. Altogether, young leaves produced foliar nectar from the second to about the 18th week; at this time leaves were fully lignified and showed a dark green tint.

Active EFNs occurred very early in the ontogeny of *P. pinnata*: saplings less than 30 cm in height already produced extrafloral nectar and thus attracted various ants nesting in the vicinity of the plant (Fig. 1). On small plants, devoid of domatia, we recorded EFN visitors of the following ant subfamilies and genera: Myrmicinae (*Crematogaster*, *Cataulacus*, *Meranoplus*, *Monomorium*, *Myrmecaria*); Dolichoderinae (*Dolichoderus*, *Technomymex*, *Tapinoma*, *Philidris*); Formicinae (*Anoplolepis*, *Oecophylla*); and Pseudomyrmecinae (*Tetraponera*).



Fig. 1. *Myrmecaria* ants at extrafloral nectary (EFN) of a small sapling of *Pometia pinnata*. **A:** young leaf – about one week old – with the basal first and second pair of leaflets already developed; scalebar 5 mm. **B:** ant at the active EFN on the underside of a leaflet (second pair); scalebar 2 mm.

The leaf domatia

The compound, paripinnate leaves of *P. pinnata* consisted of 3–13 pairs of leaflets (Fig. 2 A,B). The ant-housing structures were formed by the persistent first (basal) and second pair of leaflets. Whereas the large apical leaflet pairs (14.5–34 cm in length) were horizontally spread more or less sideways (90° – 120°) from the leaf rachis, the first two basal leaflet pairs were distinctly modified in size, shape, and spatial orientation. They were strongly reduced in size, asymmetrically formed because of the reduced growth of one half of the leaflet blade, and reflexed back to the stem where the leaf was borne.

The greatest modification was observed in the first basal pair of leaflets (length 0.4–3.6 cm and 1.5–6.5 cm in juvenile ($n = 31$) and adult plants ($n = 38$), respectively). They were stipule-like (pseudostipules), strongly falcate and, by clasping the twig, formed a bowl-like chamber (Fig. 2 C). The similarly but less strongly modified second leaflet pair (length 0.8–5.9 cm in juvenile ($n = 36$) and 2.5–9.0 cm in adult plants ($n = 40$)) built another layer of shelter above the first leaflet pair. The resulting chambers were not completely closed on all sides but ants nesting in these structures were usually able to seal the remaining gaps with ‘ant carton’ (see below; Fig. 2 D). In large leaves with ten or more pairs of leaflets, the third leaflet pair

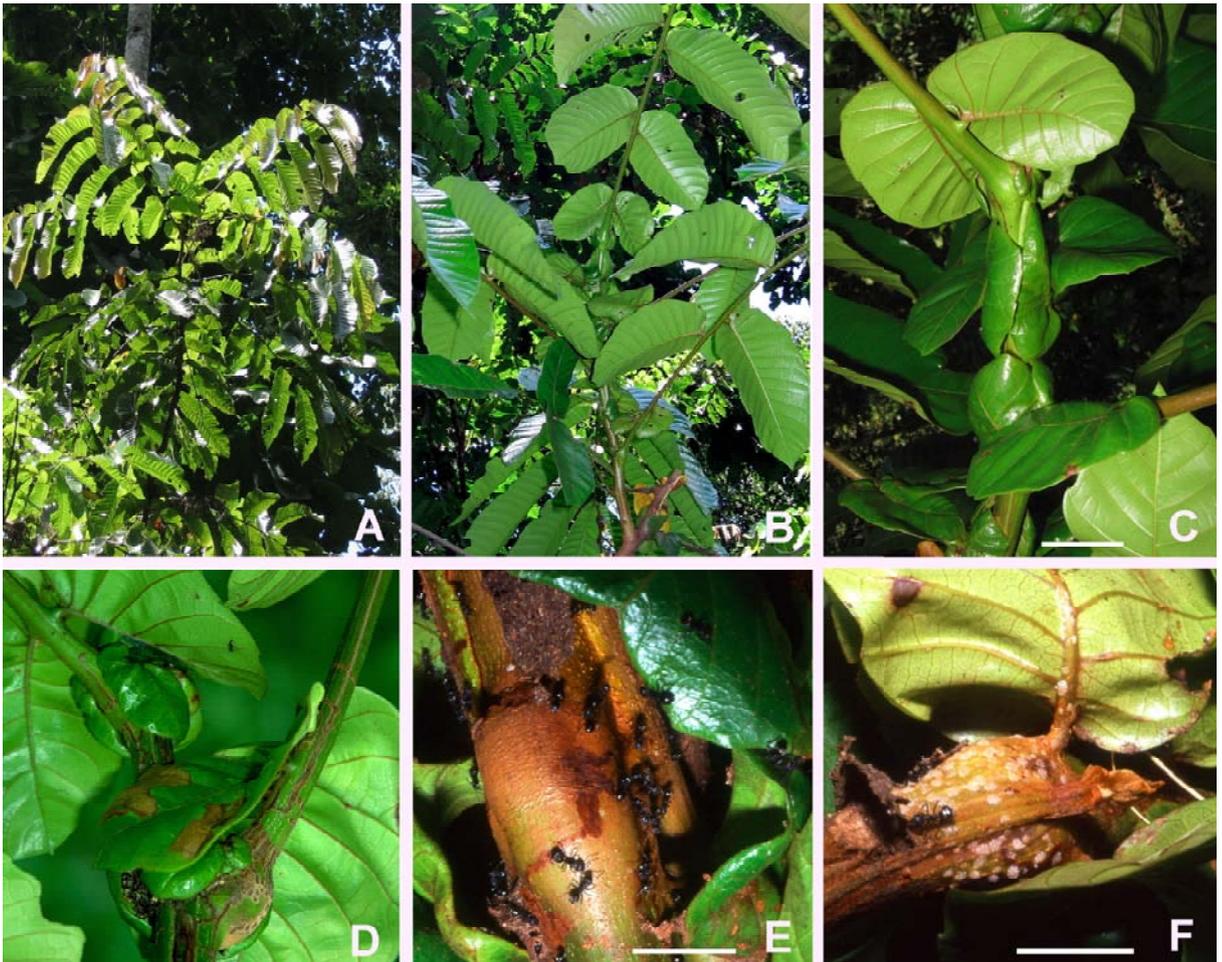


Fig. 2. *Pometia pinnata*. **A:** habitus, Ulu Gombak, Selangor, Malaysia. **B:** branch with pinnate leaves. **C:** leaf domatia, basal leaflets clasping the stem; scalebar 2 cm. **D:** ant nest under leaf domatium; note the carton with which the gaps are sealed. **E:** *Dolichoderus* ants, leaf domatium and carton material removed; scalebar 1 cm. **F:** leaflet lifted to show the trophobiotic coccids on the stem; scalebar 1 cm.

(3.0–14.5 cm in length, $n = 39$) was also slightly modified and formed a rather open ‘roof’ above the preceding pair, thus taking a minor part in the domatium formation.

At the distal end of the branches, especially in larger trees, the leaves were often set closely so that the pseudostipules of several leaves formed a more or less continuous row of domatia along the apical branch section (Fig. 2 C).

When do the leaf domatia appear? Because the basal leaflets develop prior to all other leaflets of a leaf the domatia can be utilised by ants at a very early stage of leaf development. However, the number, size and shape of the domatia, thus the availability as nesting space, were dependent on tree size. Small trees less than 2 m in height were mostly unbranched and did not yet form basal leaflets suitable as domatia. Although the pseudostipules were similarly modified and spatially oriented like those of larger trees, they were too small and not yet attached to the surface of the thin stems. Only from a height of 2 m onwards did trees begin to develop closed domatia large enough to become occupied by ants, and all trees exceeding 4 m possessed ant-housing structures.

Ant inhabitants

With increasing plant size and the development of leaf domatia, *P. pinnata* was increasingly inhabited by ants living on the trees. In total, 74.7% of trees bearing domatia ($n = 79$) were colonised. Of the 41 ant species encountered in leaf domatia, 28 (68%) were found together with brood, i.e. are confirmed ‘nesting ants’ (Appendix 1).

Among the ants sampled, the most common ‘nesting ant’ species were *Dolichoderus* sp. 1 (on $n = 10$ trees), *Philidris* sp. ($n = 8$), *Camponotus* (*Karavaievia*) *gombaki* Dumpert ($n = 6$), *Camponotus* sp. 1 ($n = 6$) and *Technomyrmex* sp. 1 ($n = 4$).

In addition to the leaf domatia formed by the plant, we found another type of ant-inhabited leaf hollows that were produced by boring insect larvae: empty tunnels, 1–2.5 cm in length, within the leaf rachis. Such holes were commonly found in widely varying numbers on 90.5% of the domatia-bearing trees ($n = 79$). A small proportion (17%) of these tunnels were inhabited by ants of a great variety (37 species), of which 22 species nested

exclusively in the leaf borer tunnels and were never found occupying the leaf domatia (Appendix 1).

In sum, the ant fauna encountered on the studied plants consisted of 63 ant species from 18 genera and 4 subfamilies.

Structure of ant nests within the domatia

Unlike stem domatia, the bowl-like chambers of the multi-leaved domatia of *P. pinnata* were incompletely enclosed and the leaflet margins had only loose contact with the surface of the stem, thus leaving open gaps that are hard to defend by ants occupying these structures. Nevertheless, seven ant species (17% of those found in domatia) used these chambers unmodified as a shelter or, rarely, as nesting space: *Dolichoderus sulcaticeps* (Mayr), *Dolichoderus* sp. 2, *Camponotus* sp. 3, *Polyrhachis* sp. 2, *Paratrechina* sp. 2, *Technomyrmex* sp. 10 and *Myrmecaria* sp. 2. Most (80.5%) of the domatia-inhabiting ants, however, additionally used carton material for improving the leaf domatia hollows (Fig. 2 D, E). They either simply closed the open gaps with ant carton (e.g., *Dolichoderus* sp. 1, *Pheidole* sp. 3, *Technomyrmex* spp. 3 and 5) or additionally enlarged the nesting space by carton chambers (*Crematogaster* spp. 11, 13, and 15, *Philidris* sp. 1, *Pheidole* sp. 2 and 3, *Technomyrmex* spp. 5 and 8, *Tapinoma* sp. 2), and/or subdivided the domatia hollows with carton walls (*Technomyrmex* sp. 1 and 8, *Crematogaster* sp. 14, *Tapinoma* sp. 6). Six colonies of the weaver ant *Camponotus* (*Karavaievia*) *gombaki* and one colony of *C. (K.) striatipes* Dumpert used carton stabilised with larval silk for closing gaps and connecting domatia chambers. These colonies could be very large, extending onto neighbouring *P. pinnata* trees or other tree species, on which they built carton silk nests beneath leaves in their typical manner (Maschwitz *et al.* 1985).

Occupation frequency of leaf domatia

The proportion of leaf domatia per tree occupied by ants was censused in 45 trees (3.0–15 m tall). On average, 70.3% (± 27.5 SD, median 71.4%) of the available domatia harboured ants but the occupation frequency varied markedly among trees. Apparently, this variation was not tightly linked to tree height, however, smaller plants

tended to have a greater mean occupation frequency of their domatia than taller plants: 88.1%, 82.8%, 57.4%, 65.5%, 63.4%, and 59.3% for the size classes 3–4.5, 4.5–6, 6–7.5, 7.5–9, 9–11, 11–15 m height, respectively.

Trophobionts and other herbivores

About 40% of all ant species sampled (26 of 63) were associated with trophobiotic scale insects, all but one of these being (unidentified) coccids (Fig. 2 F). The proportion of ant species tending trophobionts was distinctly greater in ants ‘nesting’ in leaf domatia than in leaf rachis cavities. Of the former, 64% (18 of 28) kept trophobionts within the leaf domatia or in carton shelters close to the domatia, where the coccids sucked at the stem. In contrast, only a few ant species living in rachis hollows tended trophobionts inside their tunnels (12%, 4 of 33; Appendix 1).

We did not systematically search for insect herbivores on *P. pinnata* but did observe limacodid, lycaenid, nymphalid and saturniid caterpillars as well as chrysomelid beetles feeding on young developing leaves. Other herbivores encountered were thrips, tetranychid mites and various hemipterans.

Ant activity

On juvenile *P. pinnata* trees still devoid of domatia, young leaves with active EFNs were much better patrolled by visiting ants than mature leaves or trunk sections (Fig. 3; Friedman’s test, $n = 24$, $\chi^2 = 44.3$, $df = 2$, $P < 0.0001$). This result is consistent with observations on adult *P. pinnata* trees where nesting ants preferentially patrolled young leaves for foliar nectar (data not shown).

Anti-herbivore protection of young plants by visiting ants

There was no significant difference in leaf area loss between young leaves of juvenile plants visited by ants and plants from which ants were excluded (Fig. 4; Mann-Whitney U-test, $n_{control} = 37$, $n_{experimental} = 35$, $U = 566.5$, $P = 0.36$). This result on leaf area loss, however, did not take into account whole missing leaflets. If the number of missing leaflets is analysed separately the difference between control and experimental plants is significant (Fig. 5; Mann-Whitney U-test, $n_{control} = 37$, $n_{experimental} = 35$, $U = 437$, $P = 0.018$), i.e., plants with free ant access to EFNs lost, on average, $3.2\% \pm 7.1$ leaflets (median 0), whereas plants with ants

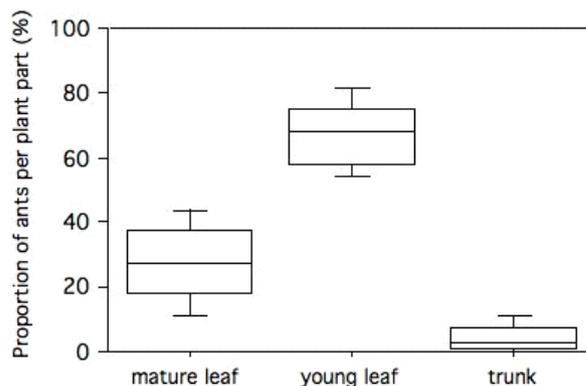


Fig. 3. Ant activity on *Pometia pinnata*: proportion of ants on three different plant parts, measured on six domatia-free treelets during two 24-h cycles (incl. one rainy day). In each plant, one young, one mature leaf and one 40 cm long trunk section was selected. Young leaves had abundant active EFNs. *Box-whisker plot*: centre line denotes median value, the box encloses the inner two quartiles (25th and 75th percentile), and the whiskers display the 10th and 90th percentile.

excluded suffered from a mean leaflet loss of $14.3\% \pm 18.3$ (median 0). It must be noted, however, that the cause of their absence could not be determined.

Anti-herbivore protection in plants with ant-inhabited leaf domatia

The overall difference in leaf herbivory between trees with ‘nesting ants’ or ‘visiting ants only’ was not significant (Mann-Whitney U-test, $P = 0.33$;

see Table 1 for detailed statistic). But because we selected trees with established ant colonies we were able to explore the anti-herbivore effect of particular ant species (Table 1). The unoccupied, domatia-free juvenile plants ($n = 18$) had a significantly higher proportion of leaf area loss (Table 1) than older plants whose domatia were inhabited by established colonies of *Camponotus gombaki* ($P < 0.05$) or *Pheidole* sp. 3 ($P < 0.05$). For the ant species *Crematogaster* sp. 3 and *Technomyrmex* sp. 1 no significant effect could be

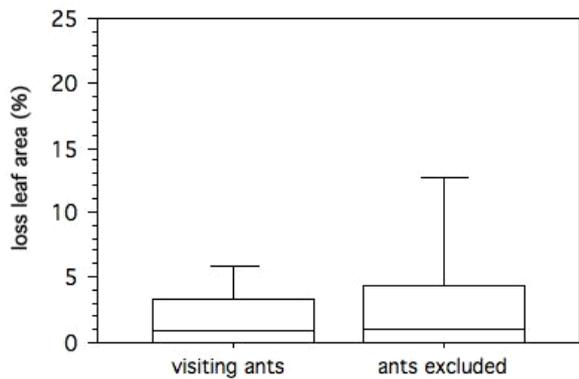


Fig. 4. Leaf area loss in *Pometia pinnata*: juvenile plants without domatia. Leaf herbivory measured after 4 weeks on young developing leaves. Categories were ‘visiting ants’ (access of tourist ants to EFN allowed; $n = 37$ leaves from 25 plants) and ‘ants excluded’ (ant access to leaves prevented with tangle trap; $n = 35$ leaves from 26 plants). [For explanation of box-whisker plot see Fig. 3.]

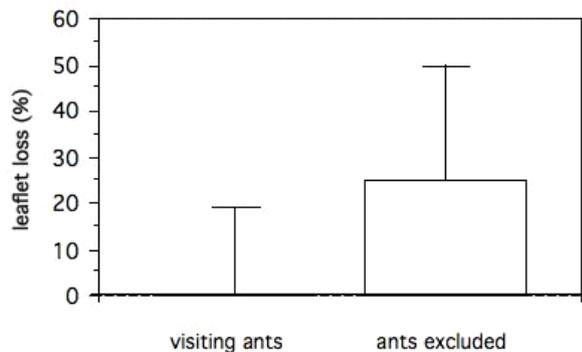


Fig. 5. Loss of leaflets in *Pometia pinnata* (pooled data): juvenile plants ($n = 51$) without domatia. Leaflet loss measured after 4 weeks on young developing leaves. Categories were ‘visiting ants’ (access of tourist ants to leaf EFN allowed; $n = 37$ leaves from 25 plants) and ‘ants excluded’ (ant access to leaves prevented with sticky resin; $n = 35$ leaves from 26 plants). [For explanation of box-whisker plot see Fig. 3.]

detected ($P = 0.09$, and $P = 0.08$, respectively). In contrast, the presence of the dolichoderine *Philidris* sp. 1 had a highly significant but positive effect on leaf area loss ($P < 0.01$).

The damage level to the leaf rachis caused by stem-borer larvae was apparently affected by the density of nesting ants. While ‘strongly’ occupied trees ($n = 21$) had, on average, $10.8\% \pm$

11.6 damaged leaf rachae, those of ‘weakly’ occupied trees ($n = 12$) had a higher mean damage level of $23.8\% \pm 21.3$ (two-tailed U-test; $U = 70.5$, $P < 0.05$, Fig. 6). Because the two groups of trees did not differ significantly in height or age of tested leaves, it is assumed that this difference in damage levels is not caused by a greater accumulation of rachis damage over time.

Table 1. Proportion of *Pometia pinnata* leaves assigned to four defoliation levels compared between domatia-free plants visited by ants and domatia-bearing plants with nesting ants; significant differences ($P < 0.05$, two-tailed U-test) are given in bold, see text. Defoliation levels: 1 (0-10%), 2 (11-25%), 3 (26-50%), 4 (>50%). Asterisks: * *Philidris* has a positive effect on leaf area loss.

Defoliation level:	1	2	3	4	<i>n</i> leaves	<i>n</i> trees	U-test
visiting ants:	59.5	30.2	8.1	2.4	86	18	
nesting ants:							
pooled	64.4	27.8	5.9	1.9	374	6	U = 15167.5 P = 0.3327
<i>Camponotus gombaki</i>	72.5	22.6	3.8	1.1	182	3	U = 6723.5 P = 0.0226
<i>Crematogaster</i> sp. 3	76.9	19.2	3.9	0	26	1	U = 910.5 P = 0.0928
<i>Pheidole</i> sp. 3	77.6	16.4	4.5	1.5	67	1	U = 2356.5 P = 0.0194
<i>Philidris</i> sp. 1	28.6	54.8	11.9	4.7	42	1	U = 1261.5 *P = 0.0023
<i>Technomyrmex</i> sp. 1	43.9	42.1	10.5	3.5	57	1	U = 2075.5 P = 0.0847

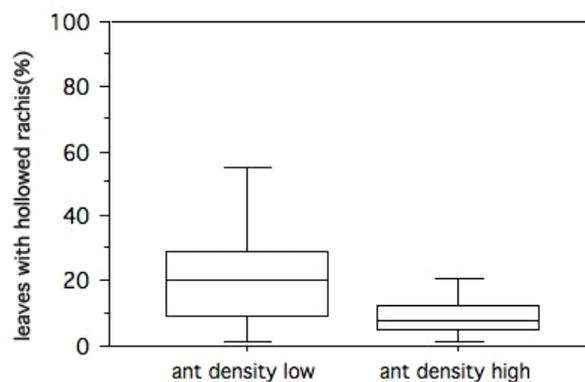


Fig. 6. Proportion of *Pometia* leaves with damaged (hollowed) rachis compared between domatia-bearing plants with ‘strong’ ($n = 21$ trees) and ‘weak’ ant density ($n = 12$ trees). [For explanation of box-whisker plot see Fig. 3.]

Pseudostipules in *Lepisanthes*: a similar case?

Four trees of *Lepisanthes amoena* could be examined at the study site. The long, imparipinnate leaves of these trees consisted of more than 20 pairs of leaflets. Compared to the other leaflets, the basal leaflets were strongly reduced in size (1.5–7 cm) and orbicular to ovate with a truncated or deeply cordate base. As in *Pometia*, the reflexed pseudostipules formed a bowl-like chamber with the margins loosely attached to the stem. The pseudostipules were connected with the normal leaflets by two or three intergrades which, however, were only marginally modified in size and shape. In three of the four trees, we found ants inhabiting the pseudostipules, one *Crematogaster* and two *Camponotus* species. Neither extrafloral nectaries, nor the glandular-pitted warts described by Adema *et al.* (1994), could be observed on the leaf lamina.

DISCUSSION

Ant rewards: leaf domatia and extrafloral nectaries

Pometia pinnata forma *glabra* possesses a complex structure of strongly modified leaflet pairs that acts as ant housing. In larger trees, the closely set leaves of the distal branches further enhance the suitability of the leaf domatia as ant domiciles. They form a more or less continuous row of spacious shelters suitable for occupation by large ant colonies.

A flush first produces the persistent stipule-like basal leaflets, and secretion of extrafloral nectar starts after the first week of emergence. Floral nectar production continues until the leaf is fully mature. We have shown that ants preferentially patrol young leaves for nectar and regularly utilise the chambers formed by the first leaflet pairs as nesting sites or shelters in which they tend trophobiotic scale insects. These findings suggest that the primary function of the modified leaves is to provide – in close proximity to food – permanent housing for ants that potentially reduce young leaf herbivory. However, the degree of specialisation of a certain plant structure to house ants is notoriously difficult to assess, especially

in facultative ant/plant associations (e.g. Davidson & McKey 1993; Moog *et al.* 2003), because ants have the natural tendency to utilise any available structure in their surroundings. During ontogeny the pseudostipules of *P. pinnata* forma *glabra* may first serve as protective envelope for the still undeveloped leaf. The relative importance of these two functions – leaf-bud cover and ant-housing – is open to speculation but the former appears less important because the pseudostipules only loosely and partially cover the subsequent leaf bud and persist after the leaf bud sprouts and matures.

The relationship with ants alters during plant ontogeny

This study demonstrates that the relationship of *P. pinnata* with ants changes during plant ontogeny from a ‘myrmecophilic’ stage in juvenile plants, in which ants are furnished with food (EFN) but no housing, to a ‘myrmecophytic’ stage in older plants (from 2 m in height onwards) in which ants are provided with both domatia and food: directly via extrafloral nectar and indirectly via excretions of associated trophobionts. Although domatia are already produced at the beginning of the leaf growth process, they are not yet suitable as a nest site resource in juvenile plants.

An ontogenetic change from a myrmecophilic to a myrmecophytic stage has also been described from the Southeast Asian pioneer tree *Zanthoxylum myriacanthum* Wall. ex Hook. f. (Moog *et al.* 2002). In *Zanthoxylum* the onset of domatia development – hollow stems giving access to ants by producing self-opening slits – occurs in plants from a height of 4 m onwards. The formation of opening slits is usually restricted to horizontal branches, whereas the vertical stem axis bears no or few slits. In addition, the number of slits on branches increases strongly with increasing distance from crown-supporting structures. Moog *et al.* (2002) suggest that the late formation of entrance slits in the fast growing ant-tree is governed by the damage risk caused by providing self-opening domatia; the latter weaken the mechanical stability of the stem significantly. Such reasoning cannot be applied to the *Pometia* system because leaf domatia do

not play a role in tree statics. What factors then affect the timing of the first appearance of the leaf domatia? Generally, plant structures such as twig diameter and size of associated leaves increase during plant ontogeny, at least from the seedling to the pre-reproductive stage. Thus ants colonise plants only at later stages of development, when leaf domatia have reached a threshold size. Assuming that the expression of domatia later in development is the primitive condition, we may ask why precocity of the onset of domatia has not been evolutionarily favoured, as it has in *Macaranga* with stem domatia (Fiala & Maschwitz 1992; Brouat & McKey 2000). One reason may be the absence of constant and stable pairs of interacting species, resulting from the ‘openness’ of the leaf domatia to a large set of arboricolous, generalist ants. The high variation in costs and benefits (see below) has probably hindered the increasing specialisation of ants and the plant.

Ants using leaf domatia as nest sites

Does the identity of ants associated with *P. pinnata* vary according to plant size – in particular, between the myrmecophilic and myrmecophytic stage? In our study the ant fauna of older plants nesting in the domatia was characterised by ants capable of producing carton (sometimes reinforced with silk) – because the domatia are not fully enclosed chambers and thus the gaps must be sealed in order to become a secure nest site. Ant species building carton nests, galleries or pavilions are a predominant element of the canopy ant community in Southeast Asia (Weissflog 2001). Taxa included dolichoderines of the genera *Dolichoderus*, *Philidris*, *Tapinoma* and *Technomyrmex*, myrmecines of the genera *Crematogaster*, *Monomorium* and *Myrmicaria*, as well as formicines of the genera *Camponotus* and *Polyrhachis*. Most of these cultivate trophobionts in their nests. The domatia are also suitable as nesting spaces for ants, such as certain species of *Camponotus*, *Crematogaster* and *Dolichoderus*, which do not build free-standing or hanging pavilions but use hollow plant structures for nesting by sealing the gaps with carton material. All these carton-building species combined constituted only a minor part in species, and presumably abundance, of the ant fauna of juvenile plants belonging to the myrmecophilic stage.

Roughly one-third (30%) of all available leaf domatia per tree were unoccupied by ants, indicating they are not a limiting resource. Residents of leaf domatia also included non-carton-building ant species that did not seal the open gaps of the domatia. They might be expected to experience strong interactions with competing ants (Way & Bolton 1997), but since we did not study the duration of domatia occupancy by different ant species we were unable to assess whether non-carton-building ants were competitively dominant and thus less in need of physical protection, or whether they were replaced by competing ants after a short time.

Protection of an ant-plant by opportunistic ants

Our results could not demonstrate that ants visiting juvenile plants before they develop domatia significantly reduce young leaf herbivory. Such an outcome of an ant-plant interaction mediated by EFNs and involving opportunistic ants is not uncommon, although not universal (e.g., O’Dowd & Catchpole 1983; Zachariades & Midgley 1999; Freitas *et al.* 2000). However, our short-term four-week-study likely underestimates a potential anti-herbivore effect (Heil *et al.* 2001). In addition, we excluded, as a conservative measure, missing leaflets from our analysis. When these were analysed separately, a significant protective effect of visiting ants was apparent. Although we do not know the factors causing the absence of leaflets it has been shown in another Bornean tree (*Shorea hopeifolia* (Heim) Sym.) that herbivore attacks on developing leaves can result in the abscission of leaves (Blundell & Peart 2000).

The evidence we present for the protective role of ants nesting in the domatia of adult *P. pinnata* trees is also ambiguous (Table 1). For the pooled data no significant effect on leaf herbivory was detected between nesting ants and ants visiting EFNs of neighbouring domatia-free juveniles. It should be noted, however, that the snapshot comparison in the standing level of leaf area loss was of ‘nesting ants’ with ‘visiting ants only’, not with ‘ants excluded’. Thus a potential protective effect of ant presence on leaf herbivory might have been overlooked.

Does the degree of protection vary with the identity of the ant associate? Our study suggests that ants do vary in their relative effectiveness

against leaf herbivores but we cannot exclude that due to low sample size the results could be skewed by individuals colonies and/or local factors. Two ant species, the highly aggressive and territorial formicine *Camponotus gombaki* and the myrmicine *Pheidole* sp. 3, were associated with significantly reduced leaf herbivory, while others suggested a negligible (*Crematogaster* sp. 3 and *Technomyrmex* sp. 1) or even detrimental (*Philidris* sp. 1) effect. The cause for such a positive effect of ant presence on leaf herbivory is unknown.

Such a varying outcome has also been described for the African ant-tree *Barteria nigriflora* Hook f. (Djieto-Lordon *et al.* 2004). As in *Pometia pinnata*, juvenile trees of *B. nigriflora* lack domatia because the lateral branches that bear the stem domatia develop later in plant ontogeny. EFNs, already present in the pre-domatium stage, are active on young leaves and stems and attract a range of opportunistic ants. However in that study, identity of ant associates changed predictably with plant ontogeny. Older *Barteria* saplings were occupied by either surface-nesting *Oecophylla longinoda* (Latreille) or domatia-inhabiting *Crematogaster* sp., and the latter species was the sole occupant of larger trees. These opportunistic ants provided significant protection to this myrmecophyte. Although the study could not demonstrate a significant anti-herbivore defence for the myrmecophilic, pre-domatium stage, the authors suggest that very young plants without domatia may benefit from facultative association with relatively ineffective ants, until the plant produces sufficient resources to sustain more effective and dominant, but more demanding, mutualists (Djieto-Lordon *et al.* 2004).

Our study on *Pometia* corroborates this assumption by showing that leaves of young domatia-free trees suffered from a greater loss of whole leaflets when ant visitation was prevented. Herbivory on stems may be even more costly to the plant than the simple loss of photosynthetic leaf area (Heil *et al.* 2001; Merbach *et al.* 2007). A hint for a potential protective effect against stem damage in *Pometia* is our evidence that ants nesting on domatia-bearing trees reduced damage of the leaf rachis caused by stem-borer larvae.

Plants with leaf domatia in Southeast Asia

Apart from epiphytic ant-garden myrmecophytes (Kaufmann & Maschwitz 2006), there are several ant-plants with leaf-derived structures frequently occupied by ants in Southeast Asia. They comprise species of *Actinodaphne*, *Callicarpa*, *Daemonorops*, *Diospyros*, *Lepisanthes*, *Korthalsia*, *Medinilla*, *Shorea*, *Smilax* and *Teijsmanniodendron* (Moog *et al.* 2003, and references therein; Heckroth *et al.* 2004). In Southeast Asia most plants with leaf domatia are characterised by two important traits which also hold for *Pometia*: the number of myrmecophytes within each genus is low, comprising only one or a few species, and they are inhabited by nesting opportunists (none being a specialised plant-ant).

The rattan palm genera *Daemonorops* and *Korthalsia* are an exception to that rule. (The genus *Daemonorops* is included because its comb-like interlocking horizontal spine-collars of the leaf sheath are considered here as 'leaf domatia' *sensu lato*.) The ant-rattans of the two genera show a high degree of radiation, and they are usually colonised by aggressive, specialised ant partners (Werner 1993; Mattes *et al.* 1998). The major trait explaining this difference from other Southeast Asian myrmecophytes with leaf domatia appears to be their vulnerability to herbivores. They have a single apical meristem and, consequently, damage to the meristem means death for the plant. Thus it is certainly of great advantage to such plants to have a set of effective mechanisms of defence, such as spines and pugnacious ant bodyguards (see also Di Giusto *et al.* 2001 who studied the ant/plant mutualism of the African wild yam *Dioscorea praehensilis* Benth., a perennial vine with a single apical meristem, in which ants provide protection during the most vulnerable stage of its unusual growth cycle).

In another biogeographical area, the Neotropics, plants with leaf pouch domatia are extremely common (Davidson & McKey 1993), implying that some conditions under which neotropical ant-plants evolve may be fundamentally different. One main difference is the herbivore pressure exerted by highly

polyphagous leaf-cutting ants (Rockwood 1976; Farji-Brener 2001), an ant life form absent from Asia. Leaf-cutting ants are the most important native herbivores throughout the Neotropics, where *Atta* alone cuts between 12 and 17% of leaf production in some forest ecosystems (Cherrett 1989). Several ant mutualists of neotropical ant-plants have been shown to defend their hosts against leaf-cutting ants (Jolivet 1990; Vasconcelos & Casimiro 1997; Alvarez *et al.* 2001; Schmidt 2001; Michelangeli 2003), and mobilising ants against ants is apparently an effective plant defence strategy. Although suggestive it remains to be confirmed whether the absence of leaf-cutting ants in Southeast Asia is an important factor explaining why myrmecophytes with leaf domatia are relatively rare compared to the American tropics.

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Appendix 1. Ant inhabitants of *Pometia pinnata* forma *glabra* found on 79 trees within leaf domatia and hollow leaf rachis cavities. Voucher specimens are deposited at the Senckenberg Museum, Frankfurt am Main, Germany. *Asterisks:* * with trophobiotic coccids, **ant taxa without brood.

ant taxon	no. of plants	
	domatium	rachis
Myrmicinae		
<i>Cardiocondyla</i> sp. 1		3
<i>Cardiocondyla</i> sp. 2	3	6
<i>Cataulacus</i> sp.		1
<i>Crematogaster</i> sp. 1	3*	
<i>Crematogaster</i> sp. 2		1*
<i>Crematogaster</i> sp. 3	1*	
** <i>Crematogaster</i> sp. 4	2*	1
<i>Crematogaster</i> sp. 5	1*	
<i>Crematogaster</i> sp. 6		2*
** <i>Crematogaster</i> sp. 7	2*	1
** <i>Crematogaster</i> sp. 8	1*	
** <i>Crematogaster</i> sp. 9	1	
<i>Crematogaster</i> sp. 10	1*	
<i>Crematogaster</i> sp. 11	1*	1
<i>Crematogaster</i> sp. 12		1*
<i>Crematogaster</i> sp. 13	1*	2
<i>Crematogaster</i> sp. 14		3
<i>Crematogaster</i> sp. 15	1	
<i>Crematogaster</i> sp. 16		1
<i>Monomorium</i> sp. 1		1
<i>Monomorium</i> sp. 2	1*	3
** <i>Myrmecaria</i> sp. 1	2	
** <i>Myrmecaria</i> sp. 2	2	
<i>Paratopula</i> sp.		1
<i>Pheidole</i> sp. 1		1
<i>Pheidole</i> sp. 2	2*	
<i>Pheidole</i> sp. 3	2*	2
<i>Tetramorium</i> sp.		3
<i>Vombisidris</i> sp.		1
unidentified genus		1

Dolichoderinae		
<i>Dolichoderus sulcaticeps</i>	1*	
<i>Dolichoderus</i> sp. 1	10*	
<i>Dolichoderus</i> sp. 2	1	
<i>Philidris</i> sp.	8*	
<i>Tapinoma</i> sp. 1	1	
<i>Tapinoma</i> sp. 2		3
<i>Tapinoma</i> sp. 3		1
<i>Tapinoma</i> sp. 4		1
<i>Tapinoma</i> sp. 5	1	1
<i>Tapinoma</i> sp. 6	1	1
<i>Technomyrmex</i> sp. 1	4*	1
<i>Technomyrmex</i> sp. 2	1*	
<i>Technomyrmex</i> sp. 3	2	2
<i>Technomyrmex</i> sp. 4		1
<i>Technomyrmex</i> sp. 5	2*	1
** <i>Technomyrmex</i> sp. 6	1*	
** <i>Technomyrmex</i> sp. 7	1	1
<i>Technomyrmex</i> sp. 8	2	
<i>Technomyrmex</i> sp. 9		2
<i>Technomyrmex</i> sp. 10	2	1
** <i>Technomyrmex</i> sp. 11	1	
Formicinae		
<i>Camponotus gombaki</i>	6*	
<i>Camponotus striatipes</i>	1*	
<i>Camponotus</i> sp. 1	6*	1*
<i>Camponotus</i> sp. 2		1
** <i>Camponotus</i> sp. 3	1*	
<i>Gesomyrmex</i> sp.		1
** <i>Paratrechina</i> sp. 1		1
** <i>Paratrechina</i> sp. 2	1	
** <i>Polyrhachis</i> sp. 1	1	
<i>Polyrhachis</i> sp. 2	1	
<i>Polyrhachis</i> sp. 3	1	
Pseudomyrmecinae		
<i>Tetraoponera</i> sp.		1
sum: 63 species	41 species	37 species

ASIANMYRMECOLOGY

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