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Ficus obscura var. *borneensis* (Moraceae), a new non-specific ant-plant from Malesia

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Abstract: *Ficus obscura* var. *borneensis* is a true myrmecophyte. It spontaneously forms cavities (domatia) in parts of its twigs which open by slits. These occur in the internodes and are usually not swollen. The domatia are inhabited by a variety of non-specific tree-living ants including *Crematogaster* spp., *Cataulacus* sp., *Tetramorium* sp., *Cardiocondyla* sp. and *Camponotus* sp.. Additionally the plant provide a sugar-containing secretion from extrafloral nectaries on the lower surfaces of the leaves. Examination of herbarium specimens of 37 other South-east Asian *Ficus* species did not reveal a single specimen with domatia.

INTRODUCTION

The moraceous genus *Ficus* is one of the largest plant genera in South-east Asia. It displays a variety of unique biological features ranging from its growth behaviour to its relationships with other plant and animal species in the environment. The genus has a wide range of habits, including trees, epiphytes, stranglers and root climbers. A further fascinating feature of figs is the mutualistic aspect of their flowering biology, which is characterized by an extremely tight mutualism with a great number of species-specific agaonid wasps, which in turn are hosts to different specialised parasitic wasps. Fig fruits are of great importance in tropical ecosystems, as they form a main food source for many birds and mammals. Figs are therefore regarded as keystone species in the forest ecosystem.

Mutualistic relationships with ants also exist. Many figs possess glandular structures on the leaf or shoot, which appear to be extrafloral nectaries. In the tropical Australasian region true ant-plants in *Ficus* have not yet been verified. Jolivet (1986) reported that there are shoot cavities in *Ficus inaequalis* Ridl. from Sulawesi and in the North Australian

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F. copiosa Stued. (=*F. subinflata* Warb.), but it is not clear whether they are true ant-domatia provided by the plants or pathological gall formations.

Recently we discovered a Malesian fig, *Ficus obscura* var. *borneensis* (Miq.) Corner, which spontaneously forms open stem cavities which may be inhabited by ants. This is an example of a true myrmecophytic habit.

MATERIAL AND METHODS

Samples of *F. obscura* var *borneensis* comprised individuals from the following sites: two specimens growing as epiphytes, one on a raintree *Samanea saman* close to the central office of the Forest Research Institute Malaysia (FRIM), and one at the Genting Tea Estate, Pahang; nine shrubs and trees from a heavily disturbed area near Miri, Sarawak. In addition to *Ficus obscura* var. *borneensis,* we studied herbarium specimens of another 206 species and subspecies of *Ficus* from the Australasian region. Thirty-seven species and subspecies or varieties of these were represented by 15 or more herbarium specimens each. From our observations on *F. obscura* var. *borneensis* in the herbarium, we regarded 15 specimens to be sufficient to decide if a myrmecophytic character was present. The fig species was identified using Kochummen (1978) and checked with herbarium specimens at FRIM. Tests for glucose were carried out with Dextrostix (Merck).

RESULTS

Domatia

Ficus obscura var. *borneensis* is an epiphytic or strangling fig. Its leaves have a short stalk and are unequal sided. The fruits are clustered in the leaf axils and on the bare twigs. The twigs are reddish hairy and have persistent stipules. Long sections of the younger internodes are hollow and represent domatia (Fig. 1). Domatia-bearing sections of the stem are either no swollen or very slightly swollen. The cavities as a rule can only be recognized by their openings or developing opening slits.

Observations on living plants

In nine shrubs and trees and two epiphytes, 39 branches between 40-250 cm length were investigated in detail. In 23 branches with a length of at least 72 cm and a width of more than 0.6 cm, 35 domatia were found. Eighteen branches had one, five branches had two, and two branches had three domatia. We measured 21 domatia which varied in length from 6-50 cm ($x=18.44 \pm 10.2$ cm). Domatia usually had one opening slit; three was the maximum. The opening slits had an average length of 1.95 ± 0.7 cm and a width of 0.39 ± 0.18 cm.

Nine developing slits were not yet connected with the stem cavity and five slits had closed again. Before a slit opening becomes visible, the

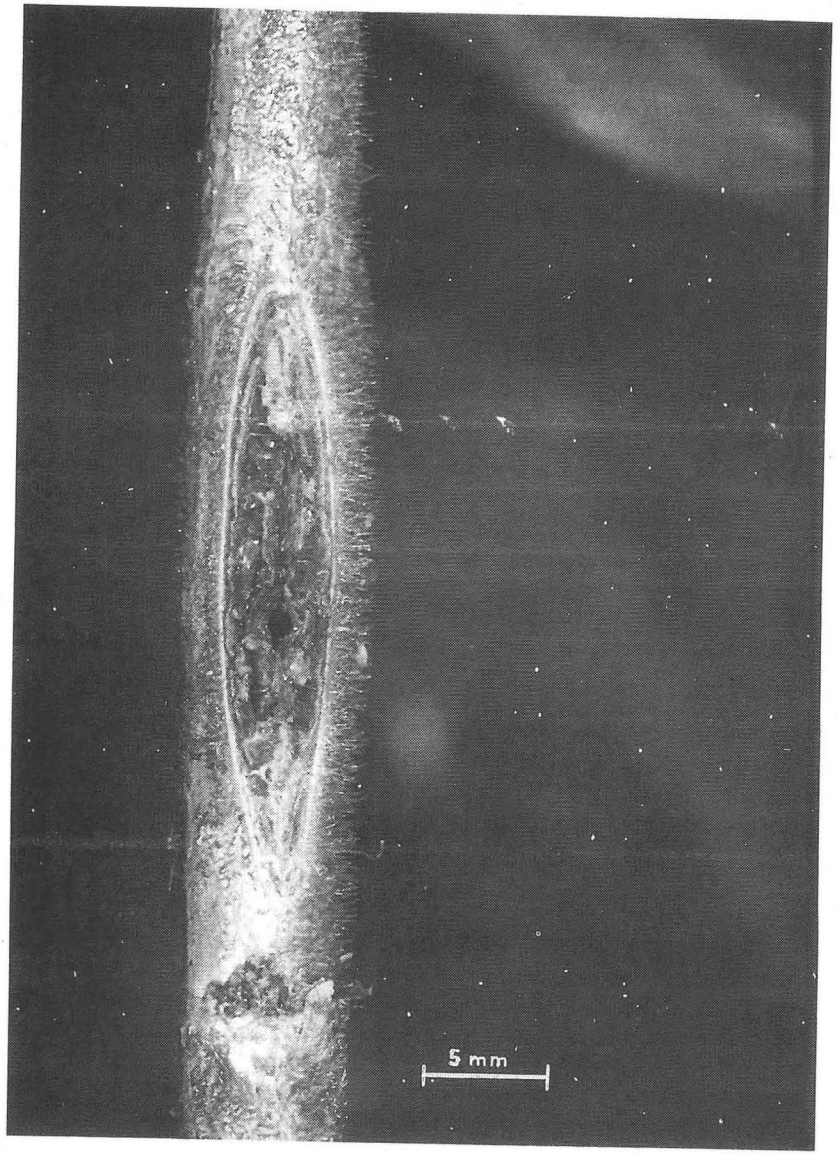

Figure 1: Domatium slit closed again by growth of the twig. *Crematogaster* sp. ants keep an entrance hole open.

stem pith degenerates, i.e. it becomes fragmented and brownish in colour before finally breaking down completely. In such stem regions, slits begin to appear as a result of normal growth processes of the plant. Where the cavities are not used by ants, the stem grows and closes the slits again.

From 56 open domatia taken from all 11 study plants, 36 (64%) were inhabited by ant colonies, colony fragments or colony founding queens, 15 were not colonized and five contained ant remains. The ant inhabitants comprised four species of *Crematogaster,* one *Cardicondyla* sp., one *Cataulacus* sp., one *Tetramorium* sp. and one *Camponotus (Colobopsis)* sp. Mealybugs were found in only two domatia, one of which contained a small ant colony, while in the other the mealybugs were visited by single workers of *Crematogaster* ants nesting elsewhere.

Extrafloral nectaries

On the lower leaf surface of *F. obscura* var. *borneensis* dark red shiny glandular structures are situated in the distal angles between the main leaf vein and secondary veins (Fig. 2). Their size diminishes from the leaf base to the tip. In the greenhouse on many of them a fluid was secreted, which formed a crystalline whitish residue when drying. With Dextrostix, the presence of high amounts of glucose could be demonstrated, proving their character as extrafloral nectaries.

Observation of herbarium material

Ficus obscura var. *borneensis*

Forty-three samples of *Ficus obscura* var. *borneensis* from the Malay Peninsula, Sabah, Sarawak, and northern Sumatra were examined. Twenty-three possessed domatia, ten of which (23%) had typical opening slits, confirming the myrmecophytic nature of this taxon.

Other varieties of *Ficus obscura*

Of the 20 specimens of *F. obscura* var. *obscura* collected from the Malay Peninsula, Sabah, Sarawak, Kalimantan, Sumatra, and the Philippines, only 6 internodes had hollow cavities without any opening slits i.e. they were not domatia. Although the sample size is small, this finding indicates that this closely related taxon is not a myrmecophyte.

Insufficient numbers of herbarium specimens of the other varieties of *F. obscura,* namely var. *angustata* (Miq.) Corner, var. *kunstleri* (King) Corner, and var. *scaberrima* (Miq.) Bl. did not allow any firm conclusions as to whether they are myrmecophytes or not.

Other Malesian and Australasian *Ficus* species

More than 20 other Malaysian fig species were examined in the field.

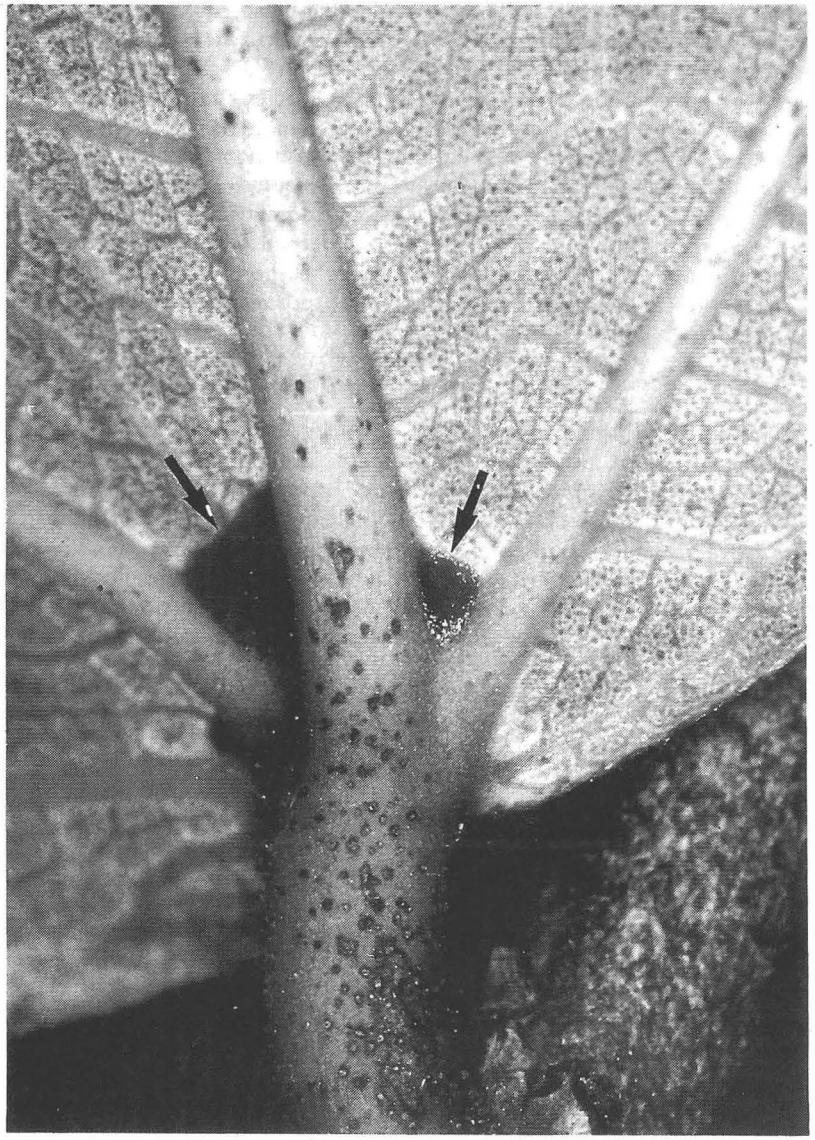

Figure 2: Extrafloral nectaries on the lower leaf surface between the midrib and side veins.

While glandular structures seem rather widespread, none of the species were found to have domatia. Several species had hollow internodes in young shoots but without opening slits.

Many herbarium specimens of different species had hollow internodes but it was not always clear whether this was an artifact of drying or not. With the exception of *F. obscura* var. *borneensis* none had any open slits, so none of the 37 taxa examined are myrmecophytes (Table 1). Nor did any of the remaining 169 species have any domatia. In *F. uniglandulosa* var. *parvifolia* (from Sarawak) among 7 internodes of a slightly swollen hollow branch one had a closed slit similar to those of closed domatia in *F. obscura* var. *borneensis*. This species also possesses extrafloral nectaries on the lower surfaces of the leaves.

DISCUSSION

Schimper (1898) interpreted slightly swollen internodes, which in part possessed slit-like openings, as ant domatia in the north Australian *Ficus copiosa* (formerly *Ficus subinflata*, e.g. Monteith 1986) and in *Ficus inaequalis* from Sulawesi. Ridley (1910) later examined these plants in the Singapore Botanical Garden over a longer period and he subsequently doubted whether these structures were true domatia. He supposed them to be gall-like pathological growths. Our observations of *Ficus obscura* var. *borneensis* showed that the hollow structures in this taxon are true ant domatia. They developed without any sign of disease or parasit infestation and were found in many plant specimens from different parts of Malaysia.

Interestingly, domatia formation is restricted only to *F. obscura* var. *borneensis*, all the other closely related varieties are completely devoid of domatia (although for some varieties, the sample sizes were small). This taxon also provides extrafloral nectar on the leaves. Extrafloral nectaries however, are also present in other varieties.

Ficus obscura var. *borneensis* is a non-specific myrmecophyte, which can be inhabited by various tree-living ants. Maschwitz *et al.* (1989, 1993, and unpublished results) have found several ant plants of the same type in South-east Asia, e.g. *Myrmeconauclea strigosa* (Rubiaceae), several species of *Zanthoxylum* (Rutaceae) and *Clerodendrum* (Verbenaceae) and one species of *Macaranga* (Euphorbiaceae). In all these species the domatia open during normal plant development. It is plausible that such structures are colonized by various opportunistic arboreal ant species. To what extent they can be regarded as starting points for the development of specific myrmecophytic systems remains an open question.

Our search for further myrmecophytic figs was not successful although we examined a great number of species, many of which had hollow young internodes. One could hypothesize that these cavities would predispose the plants for the development of specific myrmecophytic relations with

Table 1. Percentage of hollow twigs in herbarium specimens of Australasian *Ficus* species without domatia (Investigated herbarium material with a sample size more than 15).

Species	No. of Samples	% of Hollow Twigs
F. annulata Bl.	33	15
F. aurata Miq.	52	73
F. benjamina L.	22	9
F. chartacea Wall. ex King	78	41
F. deltoidea Jack	19	21
F. deltoidea var. *angustifolia*	33	15
F. deltoidea var. *intermedia*	74	53
F. deltoidea var. *kunstleri*	20	80
F. deltoidea var. *trengganuensis*	30	23
F. fistulosa Reinw. ex. Bl.	86	91
F. fulva Reinw. ex. Bl.	50	76
F. glandulifera (Wall. ex Miq.) King	35	86
F. globosa Bl.	18	11
F. grossularioides Burm. f.	42	67
F. hemsleyana King	18	11
F. heteropleura Bl.	26	15
F. hirta Vahl var. *malayana* Corner	15	100
F. hispida Linn. f.	38	79
F. ischnopoda Miq.	29	0
F. lepicarpa Bl.	69	74
F. microcarpa Linn. f.	26	35
F. mitotis Corner	16	25
F. obpyramidata King	17	94
F. oleaefolia King var. *memecylifolia*	26	15
F. punctata Thunb.	15	20
F. recurva Bl.	16	13
F. schwarzii Koord.	47	75
F. sinuata Thunb.	82	90
F. spathulifolia Corner	21	5
F. subulata Bl.	28	25
F. sumatrana Miq.	28	10
F. sundaica Bl.	57	26
F. superba Miq.	21	38
F. uniglandulosa Wall. ex Miq.	57	11
F. uniglandulosa Wall. var. *parvifolia* Miq.	26	27
F. variegata Bl.	21	52
F. vasculosa Wall. ex Miq.	20	0

specialized plant ants. However, the sticky latex produced by all figs could possibly prevent such a development. Extrafloral nectaries as found in *F. obscura* var. *borneensis*, which attract foraging ants with their sugar-containing secretions, apparently are common amongst fig species (Elias 1983, pers. obs). Though not proved in our case but in analogy to other well analyzed examples (Jolivet 1986), it can be supposed that ants attracted by nectar and/or nesting spaces in domatia provide protection against herbivorous animals to their host plants.

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