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To cite this article: W. Federle , B. Fiala & U. Maschwitz (1998) Camponotus (Colobopsis) (Mayr 1861) and Macaranga (Thouars 1806): a specific two-partner ant-plant system from Malaysia, Tropical Zoology, 11:1, 83-94, DOI: [10.1080/03946975.1998.10539354](https://doi.org/10.1080/03946975.1998.10539354)

To link to this article: <http://dx.doi.org/10.1080/03946975.1998.10539354>



Published online: 01 Aug 2012.



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***Camponotus (Colobopsis) (Mayr 1861)* and *Macaranga (Thouars 1806)*: a specific two-partner ant-plant system from Malaysia**

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Received 11 November 1996, accepted 5 September 1997

Within the paleotropical tree genus *Macaranga* (Thouars 1806) (Euphorbiaceae), the majority of ant-plant species are associated with specialized *Crematogaster* (Lund 1831) partner ants from the subgenus *Decacrema* (Myrmicinae). We have now discovered a completely different myrmecophytic system in which an ant species of the Formicinae lives in symbiosis with the peat swamp forest tree *Macaranga puncticulata* (Gage 1922). *M. puncticulata* twigs develop spacious cavities (domatia). An undescribed *Camponotus (Colobopsis)* (Mayr 1861) species of the *C. saundersi*-group was the dominant ant inhabitant (65% of the investigated plants) at forest sites, but this species, provisionally named *C. (Colobopsis)* sp. 1, was only rarely found at open stands. Another 29 opportunistic stem-nesting ant species were collected less frequently. None of them were *Crematogaster (Decacrema)* ants. *C. (Colobopsis)* sp. 1 has never been found to nest away from *M. puncticulata*. The mated queens are capable of locating young *M. puncticulata* plants and of chewing entrance holes into the domatia. In contrast to all the other obligate plant-ants associated with *Macaranga*, *C. (Colobopsis)* sp. 1 never cultivates any trophobionts, neither inside nor outside the domatia. Instead of taking up honeydew from coccids, the ants obtain carbohydrates from extrafloral nectaries along the leaf margins of *M. puncticulata*. This food source is an uncommon trait within *Macaranga* myrmecophytes. The association of *C. (Colobopsis)* sp. 1 with *M. puncticulata* is therefore the first record of a two-partner ant-plant system without endophytic coccids in the genus *Macaranga*.

KEY WORDS: ant-plant system, myrmecophyte, specificity, *Macaranga puncticulata*, *Camponotus (Colobopsis)*, Malaysia.

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INTRODUCTION

In the tropical rain forests of SE Asia, ant-plant associations have so far been little investigated. In recent years, increasing efforts have revealed a variety of new ant-plant species (e.g., MASCHWITZ et al. 1989, 1991, 1992, 1994a, 1994b; MASCHWITZ & FIALA 1995), and first experimental studies have been conducted on associations between *Macaranga* trees and *Crematogaster* ants (FIALA et al. 1989, FIALA & MASCHWITZ 1990). Even in the rather well investigated ant-plant genus *Macaranga*, we are still finding hitherto unknown myrmecophytic systems, recently in *M. lamellata* (Whitmore 1974) (MASCHWITZ et al. 1996) and now in *M. puncticulata*.

Macaranga trees are common pioneer plants growing in secondary habitats like forest gaps and road sides. Most of the myrmecophytic *Macaranga* trees (24 species in West Malaysia and Borneo) are colonised by ants of a species complex of the *Crematogaster*-subgenus *Decacrema*, which comprises at least eight probably closely related species (FIALA et al. 1994; B. FIALA, A. JAKOB & J.T. LONGINO unpubl. res.). These ants nest exclusively inside the hollow stems of their *Macaranga* hosts. They feed on food bodies produced on the plant surface and on honeydew from coccids, which they cultivate inside the stems. Although extrafloral nectaries are widespread in the genus *Macaranga*, they are reduced in many obligate ant-plant species, probably as a consequence of the presence of trophobionts (FIALA & MASCHWITZ 1991). *Macaranga*/*Crematogaster* associations can therefore be considered as symbiotic three-partner systems. The *Crematogaster* ants fully depend on their host plants and are not capable of surviving without them (FIALA & MASCHWITZ 1990). They effectively protect *Macaranga* against herbivore damage and climber infestation (FIALA et al. 1989).

Here we introduce the obligatory association between *M. puncticulata* and a *Camponotus* (*Colobopsis*) species, which differs in many respects from all other known *Macaranga* ant-plant relationships.

MATERIALS AND METHODS

M. puncticulata (Gage 1922) is a shrub or small tree, up to 20 m tall, growing in lowland swamp forests of Malaysia and Borneo. It is a member of the section *Pachystemon* s. l. (WHITMORE 1975). WHITMORE considered *M. puncticulata* and *M. caladiifolia* (Beccari 1884) as synonyms, but our field studies have revealed many distinct morphological and physiological traits of both forms as well as a strongly different pattern of ant colonisation, so that they obviously represent different species (FIALA et al. 1996). This opinion has recently been supported by cladistic studies (DAVIES 1996).

Study area. The field observations were made during a 4 months' stay (January 1993-April 1993) in West Malaysia. Our main study site was the North Selangor Peat Swamp Forest near Sekinchan on the west coast of Peninsular Malaysia (3°30'N; 101°10'E; 10 m a.s.l.). This forest grows on wet and exceptionally acid peat soil and is characterised by a distinctive tree flora. The area had been disturbed by logging activities and is now covered with secondary forest. Average annual rainfall is about 2000 mm with two monsoon periods (peaks usually in November and April) but no pronounced dry season. The mean ground-water level lies only 40 cm under the soil surface,

and floods can occur during the monsoon seasons (PRENTICE 1990). The only *Macaranga* species occurring in the area are *M. pruinosa* (Miq. Muell. Arg. 1866) and *M. puncticulata*. We investigated 110 *M. puncticulata* plants with regard to habitat, growth form, presence of ants, ant species and stage of colony development. The plants were checked for occurrence of trophobiotic Homoptera, food bodies and extrafloral nectaries. The glucose content of the extrafloral nectar was verified by using test sticks manufactured for medical purposes (Dextrostix, Bayer). This quick test is specific to glucose, and other types of sugars have not been considered.

In order to study host specificity, we tried to colonise ant-free *M. puncticulata* trees (1-2 m tall; $n = 20$) with *Crematogaster (Decacrema)* ants originating from the syntopic *Macaranga pruinosa*. The domatia of 20 complete *Crematogaster (Decacrema)* colonies inhabiting *M. pruinosa* were cut into pieces (verifying carefully the presence of a queen) and then tied to *M. puncticulata*; 2 months later, we dissected the domatia of all the trees. The same method was applied in a control experiment, in which we transferred 20 *Crematogaster (Decacrema)* colonies from *M. pruinosa* to ant-free *M. pruinosa* trees. Voucher specimens of *C. (Colobopsis)* sp. 1 will be deposited at the Badisches Landesmuseum in Karlsruhe, Germany and at the Entomology Section of the Forest Research Institute Malaysia (FRIM), Kepong.

RESULTS

Ant-related features of M. puncticulata

Domatia. Small *M. puncticulata* saplings have slender and solid twigs (diameter ca 4 mm). At a plant height of about 30 cm, the terminal shoot immediately starts to develop a much broader stem axis with a primary diameter of ca 10 mm (50% of $n = 30$ plants between 20 and 40 cm height already had swellings; see Fig. 1). The smallest plant found with domatia was 15 cm tall; the tallest plant that had not yet developed domatia measured 70 cm. A late development of domatia occurred only when plants had repeatedly suffered apex damages, because new lateral sprouts never formed domatium swellings until they had reached a length of ca 10 cm. The thick stem becomes hollow as a result of the complete degeneration of the pith, thus forming cavities of 2 to 7 mm inside diameter (Fig. 2). The twigs of *M. puncticulata* trees are hollow for the most part, but short stem sections remain solid without any pith degeneration. The cavities are thus divided into separate chambers ("domatium chambers"; length 2-70 cm), which do not correspond to internodes. There was no indication of the presence of prostomata or self-opening domatia, as previously reported from the closely related *M. caladiifolia* (FIALA et al. 1996). Only two irregular opening slits were found on 110 *M. puncticulata* plants.

Food bodies. *M. puncticulata* produces food bodies on the surface of all primary plant parts (except roots). They are slightly concentrated on the lower (abaxial) side of the small stipules, which are only weakly persistent. At most, three stipule pairs are present at each shoot tip. In the field, food bodies seemed to be completely absent on all plants occupied by ants. Even on uninhabited plants, only small amounts of them could be observed. On ant-free *M. puncticulata* plants grown in the greenhouse, however, food bodies were clearly visible, but their quantity (food body dry weight productivity per shoot tip) was considerably lower than that of other *Macaranga* ant-plants (P. MENKE pers. comm.). Several ant species, e.g. *Oecophylla smaragdina* (Fabricius 1775) and *Anoplolepis* cf. *longipes*, were observed to collect food bodies of *M. puncticulata*. The fact that food bodies did not accumulate on uninhabited *M. puncticulata* plants in the field is probably due to effective collecting by unspecialized, free-living foragers.



Fig. 1. — Young *Macaranga puncticulata* plants (0.29 m and 0.17 m tall). The taller treelet on the left has already developed the swollen stem that becomes hollow inside by pith degeneration. Neither plant has yet been colonised by ants.

Extrafloral nectaries (EFNs). *M. puncticulata* has prominent, pan-shaped structures (0.7-1.2 mm diameter) along the whole leaf margin (16 to 38 per leaf); such glands are also found in many other *Macaranga* species (FIALA & MASCHWITZ 1991). In many of the myrmecophytic *Macaranga* species investigated so far [exceptions *M. lamellata*, *M. pruinosa* and *M. winkleri* (Pax & Hoffmann 1914); MASCHWITZ et al. 1996, pers. obs.], these glands are only hydathodes. In *M. puncticulata*, however, they secrete a liquid containing sugar. The quick test values ranged from 0.25 g/l to the maximum reading of 2.5 g/l glucose (n = 20). The leaf margin glands of *M. puncticulata* can thus be considered as EFNs. In the greenhouse, the nectaries of ant-free *M. puncticulata*

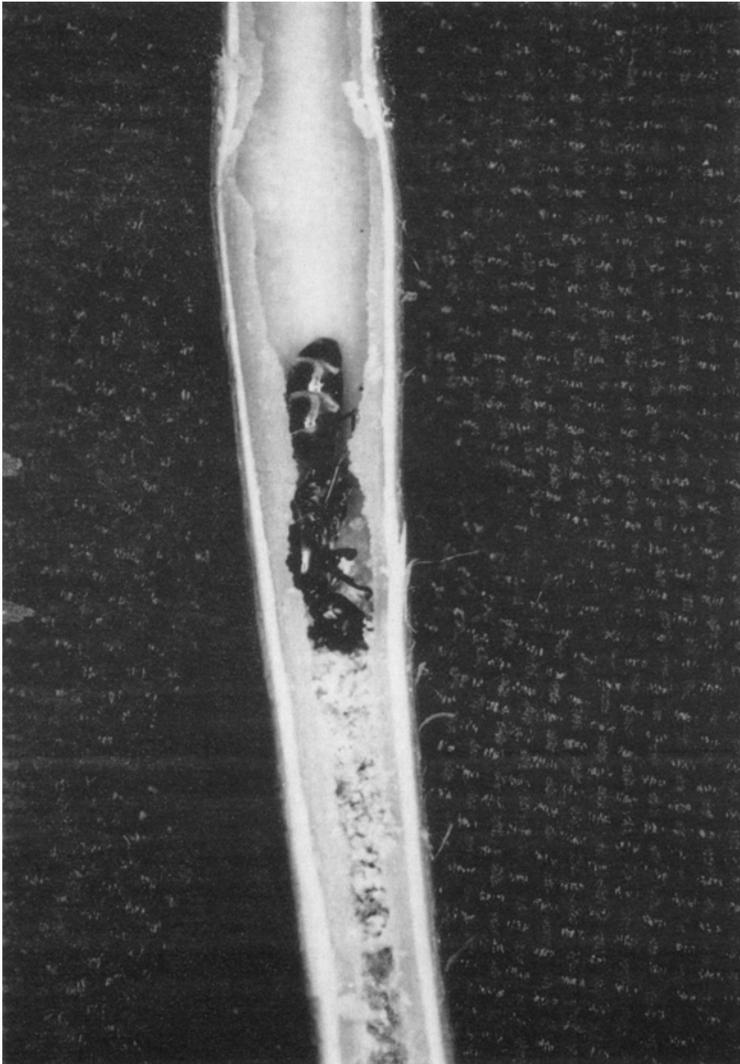


Fig. 2. — Section through a young domatium of *M. puncticulata* with a colony-founding *Camponotus (Colobopsis)* sp. 1 queen.

plants regularly became infested with fungi, a further fact confirming the presence of carbohydrates in the secretions. There are no EFNs on the leaf blade.

Ant colonisation

We found a total of 30 different ant species from the following genera nesting inside the domatia of 110 *M. puncticulata* plants (summary of all findings): *Crematogaster* (non-*Decacrema*) (7 spp.), *Paratopula* (Wheeler 1919) (1 sp.), *Pheidole* (Westwood 1839) (4 spp.), *Tetramorium* (Mayr 1855) (1 sp.), *Vombisidris* (Bolton 1991) (1 sp.), *Tapinoma* (Foerster 1850) (2 spp.), *Technomyrmex* (Mayr 1872) (3 spp.), *Camponotus*

(non-*Colobopsis*) (3 spp.), *Camponotus (Colobopsis)* (7 spp.) and *Paratrechina* (Motschoulsky 1863) (1 sp.).

The most abundant species, found on 65% of all the trees investigated at forest stands, was a *Camponotus (Colobopsis)* species, which we have provisionally named sp. 1. This *C. (Colobopsis)* sp. 1 is a so far undescribed species, which is apparently closely related (but not identical) to *C. (Colobopsis) saundersi* Emery. Both ant species are morphologically similar and share a striking defensive behaviour first reported by MASCHWITZ & MASCHWITZ (1974). When minor workers are strongly attacked, their gaster bursts and releases a sticky secretion from the hypertrophied mandibular gland sacs.

The shape of the entrance holes of colony foundation chambers indicated that the queens of only this species chew entries into the plant tissue by themselves. Moreover, we have directly observed the colony-founding behaviour of *C. (Colobopsis)* sp. 1 queens (Fig. 3, for its description see FEDERLE et al. 1998). All the other ant species, which we collected more rarely, obviously gained access to the domatia through openings that had already been present before [e.g., shoot borer holes, abandoned *C. (Colobopsis)* sp. 1 entrance holes or stem injuries caused by rodents]. Therefore, we consider those species to be opportunistic and secondary colonisers of *M. puncticulata*.

We frequently collected several colony-founding *C. (Colobopsis)* sp. 1 queens from the same young plant. Live queens were always found inhabiting separate domatium chambers; pleometrosis (plural queens per domatium) never occurred. We found a maximum number of eight queens on one plant (0.95 m tall). However, large *M. puncticulata* trees were nearly always dominated by one colony (Table 1).

We found *C. (Colobopsis)* sp. 1 to be monogynous. Large colonies live polydomously on several neighbouring *M. puncticulata* trees. For this reason, many of the plants we investigated did not contain a queen. More details about the colony structure of *C. (Colobopsis)* sp. 1 are given in FEDERLE et al. (1998).

There was a striking difference between the ant colonisation of *M. puncticulata* at shady and at open sites (Table 1). Within the shady forest stands, where most of the *M. puncticulata* plants were found, 65% of all the trees taller than 1 m were colonised by *C. (Colobopsis)* sp. 1. However, trees growing at forest edges or outside the forest were almost free of this species. At these sites, we never discovered any colony-founding *C. (Colobopsis)* sp. 1 queen on the plants investigated. This is probably due to the dominance of aggressive territorial ant species [e.g., *Oecophylla smaragdina* and *Crematogaster* cf. *artifex* (Mayr 1879)] at many of these sites. We removed five large leaf nests of *Oecophylla smaragdina* from a mass stand of 15 uninhabited *M. puncticulata* trees (> 1.5 m tall) in disturbed forest. Within the 1st week after the removal, we observed 10 *C. (Colobopsis)* sp. 1 queens colonising *M. puncticulata* [for the possible synchronization of *C. (Colobopsis)* sp. 1 nuptial flights see FEDERLE et al. 1998]. However, the colonisation of some free-standing *M. puncticulata* trees was obviously not inhibited by aggressive ants. Therefore, we also assume that swarming *C. (Colobopsis)* sp. 1 queens prefer to fly inside the forest while searching for young *M. puncticulata* plants.

As we found *C. (Colobopsis)* sp. 1 colonies to be polydomously dispersed on several *M. puncticulata* plants, we suppose that most of the plants inhabited by *C. (Colobopsis)* sp. 1 at open sites (see Table 1) were not initially colonised by queens, but by workers from colonies within denser forest.

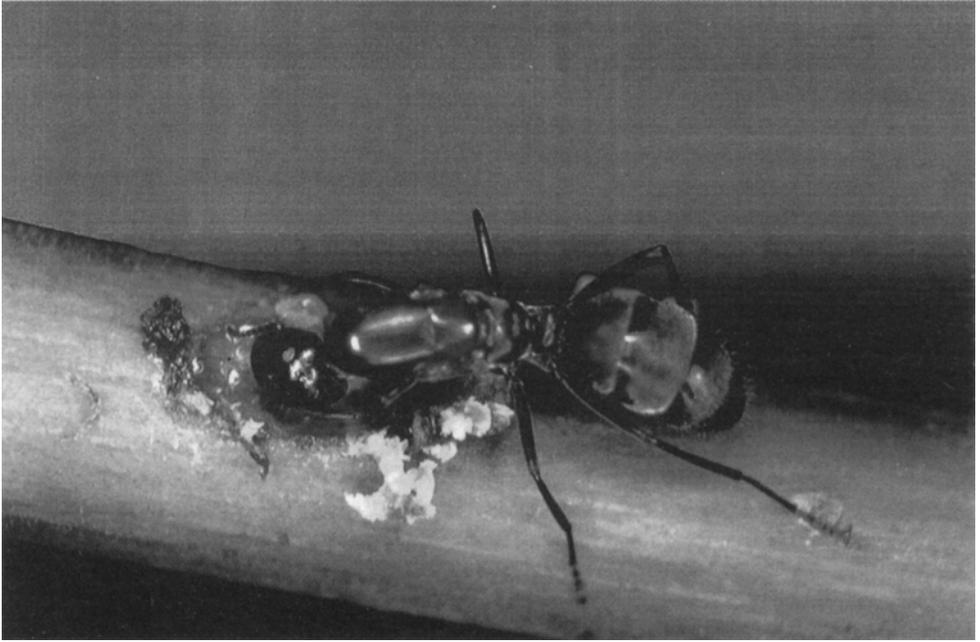


Fig. 3. — A *Camponotus (Colobopsis)* sp. 1 queen chewing her entrance hole into the domatia of a young *M. puncticulata* plant. The wings have been shed a short time before.

Table 1.

Ant colonisation of *Macaranga puncticulata*. (Only trees > 1 m tall; all the plants at open sites grew next to a forest road).

	Shady sites (n = 66 plants)	Open sites (n = 18 plants)
Not inhabited	—	50%
One dominating colony of:		
<i>C. (Colobopsis)</i> sp. 1	65%	11%
Other ant species	18%	17%
Several small colonies (of <i>C. (Colobopsis)</i> sp. 1 and/or other species)	17%	*22%

* Never *C. (Colobopsis)* sp. 1.

Host specificity

Despite thorough search (dissection of plant stems and collection of foragers), we have never found *C. (Colobopsis)* sp. 1 nesting outside *M. puncticulata*. Even the syntopic congener *M. pruinosa* was never inhabited by *C. (Colobopsis)* sp. 1 (n > 100 investigated *M. pruinosa* trees), but by two sibling species of the *Crematogaster (Decacrema)* complex. Surprisingly, none of the *Crematogaster* specimens collected on

M. puncticulata belonged to this species group. In contrast to the *Macaranga*-specialists *Crematogaster* (*Decacrema*) spp. and *C. (Colobopsis)* sp. 1, which are completely host-specific at our study site, many of the opportunistic stem-nesting ant species were found both on *M. puncticulata* and *M. pruinosa*.

The domatia of *M. pruinosa* have a relatively small inside diameter (3-4 mm), and their pith has to be excavated by the colonising ants. These factors may, at least partially, be responsible for the absence of *C. (Colobopsis)* sp. 1 on this plant. Vice versa, it is less obvious why the highly specialized *Crematogaster* (*Decacrema*) plant-ants of *M. pruinosa* never occurred on *M. puncticulata*. In order to study this problem, we tried to colonise ant-free *M. puncticulata* plants (n = 20; 1-2 m tall) with *Crematogaster* (*Decacrema*) colonies from *M. pruinosa* that contained coccids. Some 3-5 days after we had attached the "donor" twigs to *M. puncticulata*, the *Crematogaster* (*Decacrema*) workers started to chew entries into the domatia. During the following days, the colonies moved from the decaying *M. pruinosa* twigs into the domatia of *M. puncticulata*. We observed workers carrying brood and coccids into the new host plant. Many ants visited the EFNs. After 2 months, we dissected the domatia of all the trees. A few living *Crematogaster* (*Decacrema*) workers were found in only 12 of the 20 trees and the queen was still alive in only six plants. We found some young brood in the remains of only eight colonies. Pupae and larger larvae were almost absent in all the plants. Experimental control transfers of *Crematogaster* (*Decacrema*) colonies from *M. pruinosa* to *M. puncticulata* under the same conditions (n = 20) never resulted in such an outcome (19 queenright colonies with all brood stages found; differences for worker survival: $\chi^2 = 5.58$; $P < 0.05$ and presence of brood: $\chi^2 = 17.35$; $P < 0.001$).

Inside the dissected *M. puncticulata* plants, we did not find any coccids. On three plants, however, the ants surprisingly tended pseudococcids on the outer surface.

Trophobionts

C. (Colobopsis) sp. 1 never cultivated any scale insects, either inside or outside the domatia (n = 60 plants dissected). However, we found trophobionts (coccids and mealybugs) on some *M. puncticulata* plants that were colonised by other ant species (inside the domatia: n = 8, outside: n = 6).

None of the collected endophytic Homoptera was a member of the group of *Coccus* (Linné 1758) species found regularly on other *Macaranga* myrmecophytes. However, several of those *Coccus* spp. occur in the same peat swamp forest habitat living inside the domatia of *Macaranga pruinosa*. Not only *Crematogaster* (*Decacrema*) ants, but also a variety of secondary ant inhabitants can cultivate these endophytic coccids (unpubl. res.). The complete absence of coccids on *M. puncticulata* is possibly caused by unfavourable plant features. Even in the presence of *Crematogaster* (*Decacrema*) ants, these coccids seem to be unable to survive on *M. puncticulata*, as suggested by the colony transfer experiment described above.

DISCUSSION

The relationship between *C. (Colobopsis)* sp. 1 and *M. puncticulata* is a specific ant-plant association. The following points of evidence speak in favour of the specificity of the investigated myrmecophytic system:

1. The majority (65%) of all trees > 1 m inside the forest were colonised by *C. (Colobopsis)* sp. 1.
2. *C. (Colobopsis)* sp. 1 has never been found to nest outside its host plant or on any other *Macaranga* species.
3. *C. (Colobopsis)* sp. 1 colony-founding queens are capable of locating *M. puncticulata* plants precisely among many other trees in a dense forest and of chewing entrance holes into the domatia by themselves.
4. The occurrence of multiple colonisations of young plants gives evidence that there is a strong intraspecific competition for host plants.

The association between *C. (Colobopsis)* sp. 1 and *M. puncticulata* is the only two-partner system in the genus *Macaranga* known so far. In contrast to the *Macaranga* three-partner systems with *Crematogaster (Decacrema)* ants, trophobiotic coccids are completely absent.

M. puncticulata differs from many other *Macaranga* myrmecophytes by producing large quantities of extrafloral nectar. EFNs commonly occur in the non-myrmecophytic *Macaranga* species and may thus have been present in the first primitive myrmecophytes too. FIALA & MASCHWITZ (1991) suggested that the occurrence of trophobionts inside the domatia enabled the host plants to reduce their sugar secretions, so that in the course of evolution, the EFNs have lost their function. Our finding of a two-partner system without coccids and with EFNs supports this hypothesis. Possibly as a consequence of unfavourable plant properties, *C. (Colobopsis)* sp. 1 may never have cultivated Homoptera in the domatia of its host, in contrast to the *Crematogaster (Decacrema)* ants [for the trophobiosis capacity of *C. (Colobopsis)* sp. 1 see FEDERLE et al. 1998]. The extrafloral nectar of *M. puncticulata* thus stayed essential for the survival of the ant colony. *M. puncticulata* was termed a "transitional species" (being intermediate between myrmecophytic and non-myrmecophytic) by FIALA & MASCHWITZ (1992). However, the different types of ant associations in the genus *Macaranga* have proved to be much more complex than previously supposed. For this reason, we will no longer employ this term.

The association between *C. (Colobopsis)* sp. 1 and *M. puncticulata* appears to benefit both partners. *M. puncticulata* provides hollow stems as nesting space and food in the form of food bodies and extrafloral nectar. We have also shown that *C. (Colobopsis)* sp. 1 protects its host plant against herbivory and climber infestation (FEDERLE et al. 1998).

Compared with other *Macaranga* ant-plants (FIALA et al. 1989), the degree of colonisation of *M. puncticulata* by *C. (Colobopsis)* sp. 1 seems to be rather low. However, in many of our study plants, the twigs had been torn open by myrmecophagous rodents. Thus, the domatia had often become accessible for non-specific secondary colonisers. As this kind of myrmecophagy is only found locally (unpubl. res.), the degree of ant colonisation is possibly higher at other sites.

The presence of *C. (Colobopsis)* sp. 1 strongly depends on habitat factors. Habitat effects on ant-plant relationships have been observed in several ant-plant genera (e.g., neotropical *Cecropia*, African *Barteria* and *Acacia*, see DAVIDSON & McKEY 1993) and also in the Bornean *Macaranga lamellata* (MASCHWITZ et al. 1996). In contrast to all these myrmecophytic systems, there are no other specialized plant-ants replacing *C. (Colobopsis)* sp. 1 at open sites. At our study site, the ant colonisation exclusively depends on the host plant species. The plant-ants living on *M.*

pruinosa and *M. puncticulata* have never been found to colonise their syntopic congeners.

The ant-plant genus *Cecropia* is considered to be the neotropical analogue to *Macaranga*. Here, the majority of ant-plant species are inhabited by ants of the Dolichoderine genus *Azteca*, but a few additional ant genera (*Pachycondyla*, *Crematogaster*, *Camponotus*) are represented less frequently (DAVIDSON et al. 1991, LONGINO 1991). In *Macaranga*, we find a strikingly similar pattern. Ant partners of the *Crematogaster* (*Decacrema*) species complex are numerically dominant (Table 2). Only three *Macaranga* species, i.e., *M. lamellata*, *M. winkleri* and *M. puncticulata*, are known to be inhabited by specialized ants from other taxa [*M. winkleri*: *Crematogaster* (non-

Table 2.
Tabular comparison of two myrmecophytic systems in the genus *Macaranga*.

Association	<i>Macaranga</i> spp./ <i>Crematogaster</i> (<i>Decacrema</i>) spp.	<i>M. puncticulata</i> / <i>C. (Colobopsis)</i> sp. 1
Plants	<i>M. aetheadenia</i> (Airy Shaw 1974) <i>M. beccariana</i> (Merr. 1950) <i>M. calcicola</i> (Airy Shaw 1971) <i>M. constricta</i> (Whitmore & Airy Shaw 1971) <i>M. depressa</i> (Muell. Arg. 1866) * <i>M. havilandii</i> (Airy Shaw 1969) <i>M. hosei</i> (King ex Hook 1887) <i>M. bullettii</i> (King ex Hook 1887) (2 subspp.) <i>M. hypoleuca</i> (Muell. Arg. 1866) <i>M. indistincta</i> (Whitmore 1974) <i>M. kingii</i> (Hook 1887) (2 subspp.) <i>M. lamellata</i> (Whitmore 1974) ** <i>M. motleyana</i> (Muell. Arg. 1866) (2 subspp.) <i>M. pearsonii</i> (Merr. 1926) <i>M. petanostyla</i> (Airy Shaw 1971) <i>M. pruinosa</i> (Miq. Muell. Arg. 1866) *** <i>M. puberula</i> (Heine 1951) <i>M. trachyphylla</i> (Airy Shaw 1971) <i>M. triloba</i> (Muell. Arg. 1866) (+ at least two undescribed species)	<i>M. puncticulata</i> (Gage 1922)
Ants	≥ 8 <i>Crematogaster</i> (<i>Decacrema</i>) species; each of them occurring on 1 to 6 <i>Macaranga</i> species)	<i>C. (Colobopsis)</i> sp. 1
Ant diet:		
EFNs	-/+ ****	+
Food bodies	+	+
Trophobionts	+	-

* Only one out of three types of *M. depressa* is myrmecophytic. This ant-plant type corresponds either to the "forma glabra" or the "forma depressa" described by WHITMORE (1974), but can not be identified unequivocally. ** *M. lamellata* is either inhabited by *Camponotus* (non-*Colobopsis*) *macarangae* or by a *Crematogaster* (*Decacrema*) species (MASCHWITZ et al. 1996). *** We found the Bornean form of *M. pruinosa* to be morphologically different and never colonised by ants (n > 50 plants observed). **** EFNs present in *M. lamellata*, *M. pruinosa* and *M. winkleri* (MASCHWITZ et al. 1996, pers. obs.).

Decacrema msp. 8, FIALA et al. 1994; *M. lamellata*: *C. (non-Colobopsis) macarangae* (Dumpert 1996), MASCHWITZ et al. 1996]. DAVIDSON & McKEY (1993) proposed the hypothesis that in the course of evolution, competitively dominant plant-ant species (e.g., members of the genera *Crematogaster* and *Azteca*) have repeatedly replaced prior ant associates of subordinate rank (e.g., *Tetraponera* or *Camponotus* species). As higher levels of aggression require more energy input, these subordinate plant-ant species are more likely to survive in less productive habitats, where the host plants supply fewer resources for the ants. Our findings with *M. puncticulata* seem to support this model. This plant grows on relatively infertile and wet peat soil, is shade-tolerant and rather slow-growing (*M. puncticulata* 2.1 mm/day, *M. pruinosa* 4.7 mm/day; average of $n = 30$ trees 2-10 m tall of each species measured over 2 years in their natural habitats). *M. puncticulata* provides relatively small amounts of food bodies. Therefore, we conjecture that its low resource supply is not sufficient for *Crematogaster (Decacrema)* ants. Further studies are needed to quantify the resource investments of different *Macaranga* host plants.

ACKNOWLEDGEMENTS

This study was financially supported by a research grant from the Studienstiftung des Deutschen Volkes to W. Federle and by the Deutsche Forschungsgemeinschaft (DFG). We are grateful to the Department of Zoology, Universiti Malaya, for cooperation. Bernd Hahn-Schilling provided important help and valuable information for the field work at Sekinchan. We thank Hans-Peter Heckroth for identifying the coccids. We are grateful to an anonymous referee for helpful comments on the manuscript and for improving the English.

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