

# A SOUTH-EAST ASIAN MYRMECOPHYTE WITH TWO ALTERNATIVE INHABITANTS: *CAMPONOTUS* OR *CREMATOGASTER* AS PARTNERS OF *MACARANGA LAMELLATA*

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**Abstract.** In the tropical rain forest of Sarawak, east Malaysia, a new myrmecophytic three-partner system has been discovered which consists of the tree *Macaranga lamellata* (Euphorbiaceae), two alternative ants, a *Camponotus* and a *Crematogaster* species, and trophobiotic *Coccus* species. The *Macaranga* tree, which belongs to the section *Pachystemon* occurs mainly in primary lowland mixed dipterocarp forest in Sabah, Sarawak and Kalimantan. The *Crematogaster* and *Coccus* species are typical symbionts of myrmecophytic *Macaranga*. However, *Camponotus macarangae* nov. sp., herein described, has not previously been found on myrmecophytes and does not fit into any of the currently recognized *Camponotus* subgenera. While *Crematogaster* species occurred in disturbed as well as undisturbed habitats, *Camponotus macarangae* was found only in undisturbed primary forest in Sarawak, where it was more common than *Crematogaster* species. *M. lamellata* is a highly developed myrmecophyte, which produces self-hollowing domatia as a young sapling and food bodies on the lower surface of the large, recurved and enrolled stipules. Details of the nesting habits and colony structure are reported for *Camponotus macarangae*, and are shown to be somewhat different from those of typical *Macaranga-Crematogaster* associations. Colony foundation is fully claustral. The trophobiotic coccids must therefore migrate by themselves into the nest or have to be taken in by *Camponotus* workers after opening. Regularity of colonization, and modes of host plant selection and colony foundation by the *Camponotus* females, indicate that this ant is an obligate and highly developed myrmecophytic species. This is also true for the *Crematogaster* species. A possible evolutionary development of this unique system is discussed. Accepted 19 August 1996.

**Key words:** Ant-plant interactions, Borneo, *Camponotus*, *C. macarangae* sp. nov., coccids, *Crematogaster*, *Macaranga*, myrmecophytes.

## INTRODUCTION

*Macaranga* (Euphorbiaceae) is the only plant genus in tropical Asia with a substantial radiation of myrmecophytes. There are approximately 23 myrmecophytic *Macaranga* species known from the Malay Archipelago. The trees have developed a complex set of associations with ants, involving numerous plant and ant species. *Macaranga* comprises a range of species, from those not inhabited by ants to obligate myrmecophytes (e.g., Fiala & Maschwitz 1991, 1992a, b; Fiala 1996). There are three main types of association: non-myrmecophytic (but myrmecophilic) species, incipient myrmecophytes ("transitionals") and obligate myrmecophytes. The myrmecophytic species are usually associated with specific ants of the genus *Crematogaster*, which live within the stem internodes of their plant-partners where they cultivate trophobiotic coccids (Ong 1978, Fiala & Maschwitz 1990). Our recent investigations show that this myrmecophytic complex is much more

diverse, and involves a much greater variation in life types and species diversity, than formerly supposed, e.g., *Camponotus* ants of the subgenus *Colobopsis* which utilize food bodies but do not keep coccids (Federle *et al.* 1994, Fiala *et al.* 1994, Fiala *et al.*, in press).

Here we report on a three-partner system from north Borneo in which the obligate myrmecophyte, *Macaranga lamellata* Whitmore, is associated with two ant species from different subfamilies: one *Camponotus* species (Formicinae) and one *Crematogaster* species of subgenus *Decacrema* (Myrmicinae).

## STUDY SITE, MATERIALS AND METHODS

*Macaranga lamellata* was described in 1974, based on a single specimen from Sabah (Whitmore 1974). Only recently has it been collected in Sarawak, Brunei, Sabah, and East and Central Kalimantan. The field work for this study was principally carried

out in Lambir Hills National Park (Lambir), Sarawak, Malaysia (4°20'N, 113°50'E). Lambir includes 7800 ha of lowland mixed dipterocarp and tropical heath forest. The climate is aseasonal, with mean monthly rainfall >100 mm for all months. A number of plants were also studied in a logged forest adjacent to Lambir, towards the coastal town of Miri. In addition to material from Lambir, *M. lamellata* plants were found in Tawau Hills, Sabah, and in East Kalimantan. Five Central Kalimantan specimens of *M. lamellata* were studied in the Herbarium of the Royal Botanic Gardens, Kew, U.K.

Various aspects of the ant-plant-coccid association were studied in the field, including myrmecophytic characteristics, the specificity of the relationships between the plants and their ant inhabitants, and the demography of the trees. Study plots were set up in Lambir to map the distribution of the plants and monitor their growth patterns. These plots are fully described in Davies (1996, and in prep.).

Ant specimens have been deposited in the collection of the authors, and will also be deposited in the Entomology Section of FRIM, Kepong, Malaysia, and BMNH, London. Herbarium specimens have been deposited in the Harvard University Herbaria (A) and in the Kuching Herbarium (SAR) in Malaysia.

## RESULTS

### *The plant: habitat and ant-plant features*

*Macaranga lamellata* is endemic to Borneo. It typically occurs in mixed dipterocarp forest on well-drained sandstone-derived soils. Unlike most of the ant-inhabited *Macaranga* species, *M. lamellata* is quite shade-tolerant (Davies *et al.*, in prep). It is mostly restricted to primary forest, but can also be found in small forest gaps and sometimes occurs in patches of logged forest. *M. lamellata* is a small tree up to 15 m tall and 10 cm diameter at breast height (Davies *et al.*, in prep.). The new shoots and the undersides of the peltate leaves are waxy and whitish in colour (Fig. 1). The paired, elongate stipules are 2.0–2.5 cm long, recurved and horn-shaped. They bear many white food bodies on their undersurfaces (Fig. 3), as in other specialized myrmecophytic *Macaranga* species. The ants get access to these food bodies through small openings between the stipules and the stem. Food bodies are also produced along the veins on the underside of the leaves. Along the leaf margins extrafloral nectaries secrete fluids con-

taining high amounts of glucose (test with Dextrosticks for medical purpose, MERCK). These sticks differentiate only up to a maximum reading of 2.5 g/l). Seedlings, approximately 7 cm tall, begin to develop distinctly enlarged stem domatia which become hollow by themselves through pith degeneration. With the exception of the white waxy covering of stem and leaf undersides, *M. lamellata* shares numerous morphological similarities with the closely related myrmecophytic species *Macaranga kingii* var. *platyphylla*.

### *The ant occupants of Macaranga lamellata*

The majority of *M. lamellata* plants in both primary forest (97%, n = 125) and logged forest (100%, n = 30) were colonized by ants. Interestingly however, we found two very different ant species as specialized colonists as well as a number of occasional inhabitants.

#### a) *Camponotus macarangae*

We surveyed *M. lamellata* plants in a number of different sites in the primary forest at Lambir. Altogether 81% of the 121 ant-inhabited trees were exclusively occupied by a single *Camponotus* species, which is newly described below as *Camponotus macarangae*. The youngest domatium-bearing saplings, or young shoots of cut stems less than 15 cm tall, often contained colony-founding queens (Fig. 2).

The sub-generic position of *Camponotus macarangae* is not clear. Although it shares similarities with both subgenus *Colobopsis* and subgenus *Karavaievia*, it does not fit perfectly into either of these taxa (see below). *Camponotus macarangae* is distinctly different from many other *Camponotus* species in having monomorphic workers and cocoonless pupae, among other features.

#### b) *Crematogaster* (subgenus *Decacrema*) sp.

*Macaranga lamellata* was also inhabited by specialized ants of the genus *Crematogaster* (subgenus *Decacrema*). The association of *M. lamellata* with *Crematogaster* species differed between the primary and the logged forest habitats. In the primary forest, only 19% of 121 ant-inhabited plants were colonized by *Crematogaster* species, and in a few young trees both *Camponotus* and *Crematogaster* occurred together. In contrast, *Crematogaster* was found in all 30 plants studied in the logged forest site which was about 15 km from the primary forest sites.

The logged forest trees all contained one distinct *Crematogaster* species, morphospecies #5 (Fiala,

Jakob & Maschwitz, unpublished). Morphospecies #5 is typical of *Crematogaster* subgenus *Decacrema*, and is very similar to other species found in myrmecophytic *Macaranga* species (Fiala *et al.*, unpublished work). All samples originate from one study site, where they grow in sympatry with five other *Macaranga* species. Morphospecies #5 was not found in any other species at this site.

In the primary forest, *Crematogaster* females, which are necessary for species identification, could be collected from only 10 trees. Female alates were present in plants as small as 1.8 m tall. Our data concerning the species status of the primary forest *M. lamellata* - *Crematogaster* therefore are still incomplete. In five of the ten trees *Crematogaster* morphospecies #5 was identified. In the other five trees, three other *Crematogaster* subgenus *Decacrema* species were found. These species are normally associated with *M. bosei* (sp. #1, sp. #2) and *M. trachyphylla* (sp. #4). A number of other *Macaranga* species are common in the primary forest in the vicinity of *M. lamellata* (Fig. 4) including *M. kingii* var. *platyphylla*, which is mainly colonized by *Crematogaster* sp. #3, *M. beccariana* and *M. havilandii* which are both rather specifically inhabited by *Crematogaster* sp. #6, *M. trachyphylla* inhabited by *Crematogaster* sp. #4, and *M. triloba* inhabited by *Crematogaster* sp. #3. With the exception of *M. kingii* var. *platyphylla*, the other *Macaranga* species are more light-demanding with trees mostly concentrated in forest gaps.

In addition, our collections from Tawau Hills and Kalimantan also contained *Crematogaster* (*Decacrema*) species. Species-level identification of the former ant-inhabitants in the herbarium specimens at Kew was not possible. However, the size structure of the domatium holes in the five specimens indicated that these plants had been inhabited by a *Crematogaster* species.

#### c) Other ant-inhabitants

In three young *M. lamellata* trees, in which *Camponotus macarangae* females had begun founding their colonies, additional ant species were found in different internodes. These other ant species had apparently taken over internodes from where the myrmecophytic ants had died out, as we found queen remains and typical myrmecophytic openings in these internodes. The additional ant species comprised one *Pheidole* sp., one *Camponotus* species (subgenus *Colobopsis*) of the *saundersi* group, and two queens of *Crematogaster* species not in subgenus *Decacrema*.



FIG. 1. Sapling of *M. lamellata* of about 1 m.

Two small colonies of an unidentified myrmicine ant had occupied two internodes of a small tree, which also contained a colony-founding *Camponotus macarangae* queen. The rarity of these other ant-inhabitants and their modes of plant occupation clearly indicate that *M. lamellata* is normally only associated with either of the two specific host ants, *Camponotus macarangae* or *Crematogaster* sp.

#### Ecology of *Camponotus*- and *Crematogaster*-inhabited trees

The size, spatial distribution, light environment and growth rates of *M. lamellata* trees were studied in two 10-ha primary forest plots at Lambir to investigate whether there were ecological differences between *Camponotus*- and *Crematogaster*-inhabited plants. In a sample of 72 plants, 48 (67%) were inhabited by *Camponotus macarangae*, 21 (29%) by *Crematogaster* species, and 3 (4%) plants had no ant-occupant. The size-structure of the *Camponotus*-inhabited plants did not differ from *Crematogaster*-inhabited plants ( $P = 0.56$ ; Kolmogorov-Smirnov two-sample test), and all plants above 2.6 cm diameter at breast height were ant-inhabited. The spa-



FIG. 2. Colony-founding queen of *Camponotus macaranga* with a first batch of eggs inside a hollow internode of a *M. lamellata* sapling.

tial distribution of the *M. lamellata* plants in two plots is shown in Fig. 4. Nine other myrmecophytic *Macaranga* species occurred in these plots, namely *M. beccariana*, *M. kingii* var. *platyphylla*, *M. babilandii*, *M. hosei*, *M. bulletii*, *M. hypoleuca*, *M. trachyphylla*, *M. triloba* and *M. winkleri*. In both plots, *M. lamellata* tended to be more evenly distributed than the other *Macaranga* species; this is due to its greater shade-tolerance (Davies *et al.*, in prep.). Although we did not identify the ants in all *M. lamellata* trees in the two plots, there appears to be no obvious spatial patterning of trees with different ant-colonists. *Crematogaster* colonies were intermingled with *Camponotus*-inhabited plants. The higher density of *M. lamellata* in Plot 1 is at least partly due to variation in soils and drainage within the plots (Davies 1996). There was also no significant difference in the estimated light environment between the trees with different ant-colonists (Davies *et al.*, in prep.). The genus of ant-colonist was not significantly correlated with diameter growth rates over two and a half years

( $P = 0.42$ ; Mann-Whitney U-test), though unoccupied plants grew somewhat slower than ant-inhabited plants.

#### *Colony structure, ant behavior and plant-ant characters*

Larger *Camponotus macaranga* colonies always contained only one queen indicating monogyny in this species. As a rule, the females were found in the youngest internodes of the tree, in contrast to all *Macaranga-Crematogaster* associations, where they are usually found in the lower, older parts of the stem. The *Crematogaster* workers completely hollow out the compact interior of the nodes creating an uninterrupted passage inside the stem. In contrast, the *Camponotus* workers produce many partly-separated chambers in the stem interior with help of incomplete septa built out of carton material. Although the older internodes become hollow by themselves through pith degeneration, the youngest pith-containing internodes were observed to be hollowed out by the workers from the outside. In the *Camponotus*-association, and in contrast to the *Crematogaster*-systems, the workers closed the older lower entrance holes with carton (subsequently fully closed by plant growth) and keep open only two or three entrances in the youngest internodes at the apex of the stems (a similar phenomenon was reported for *Camponotus quadriceps* on *Endospermum myrmecophilum* in Australia (Monteith & Wood 1987). *Camponotus* as well as *Crematogaster* workers were observed collecting foodbodies.

In rather young and small colonies, winged sexuals (alates) were found. Males were found in a 2.5 m tall tree, a queen-right colony was found with fewer than 100 workers, and female pupae were found in a slightly larger colony in a 5 m tall tree. The development of alates in small colonies is typical of highly-developed myrmecophytic ants, which need a frequent and high output of sexuals for rapid and complete colonization of new, strongly scattered host-tree saplings (unpublished data). We have no data on the foraging behavior of *Camponotus*-workers and do not yet know whether they are exclusively restricted to their host trees.

When aggravated by humans the workers of larger colonies attacked readily by biting. At this they released a strong, highly characteristic and pleasant smell of a citral-like terpene from their mandibular glands, probably as defense and/or alarm secretion. Actually, the type of ant-colonization of a tree can

be easily detected by this odour. We do not yet know about the protective behavior of the ants, how workers behave against herbivores or against plant competitors such as climbers, or whether they clear the plant surface of epiphyllae or herbivore eggs. In two young plants, 1 and 1.2 m tall, which were observed for a few hours, workers were most common on the youngest leaf. When we checked the leaves every 30 minutes between noon and 15:00, on average 30 workers were counted on the youngest large leaf and on average three on the older leaves.

#### *Colony foundation of Camponotus macaranga*

Colony foundation, i. e., searching behavior and domatium penetration of the young queen, was not observed directly. The weak pigmentation of both females and males of *Camponotus macaranga* suggest that swarming, mating, host plant search and colonization take place during the night, as happens in *Crematogaster* species associated with *Macaranga*. Searching behavior and host plant recognition is thought to be a highly exact process. In one of the study sites the number of young plants suitable for colonization, was rather small. In an area of about 2 ha we detected only two young *M. lamellata* plants, nevertheless both were colonized by queens (see also plant density in Fig. 4).

Many colony foundations were observed in all stages of development but most of them had not been successful (40 out of 49). One sapling, 70 cm tall, contained the remains of 15 colony-founding *Camponotus* females, and in another sapling, 40 cm tall, 7 dead queens and one live queen (still in a closed chamber), were found. In both saplings a larger living colony, with many workers was also present, suggesting that the most probable explanation for the dead queens is intraspecific competition, as is observed in *Macaranga-Crematogaster* associations (Fiala & Maschwitz, unpublished data). In the case of *Camponotus macaranga* the successful colonies (with queens) appear to have moved to the youngest internodes via the plant surface, based on the observation that no open holes were present in the lower parts and that the hollow internodes were not connected.

According to our observations on different stages of colony foundation, the arriving queens must bite a hole in a young internode, then close the hole with pith remains before laying eggs. The foundation entrance hole soon begins to close by growth and finally has to be reopened when the first workers have

eclosed. The first workers are nurtured by the queen from her body resources. These workers are smaller than those of larger colonies, which is a typical feature of claustral colony-founding ants. In two closed chambers we found single queens with 2 and 3 worker pupae respectively, in the latter together with 3 eggs (Fig. 2). Very young colonies apparently do not fight seriously, as indicated by the coexistence of two open colonies with a few workers on a single plant. This seems to happen later when more and larger workers start being active on the surface.

Colony foundation and structure of *Crematogaster* sp. #5 was typical of other *Macaranga*-inhabiting *Crematogaster* species (own observations) and will therefore not be treated here in detail. Queen alates were twice found at a plant height of only 1.5 m which is unusually early for *Macaranga*-inhabiting ants.



FIG. 3. Stipule of *M. lamellata* with food bodies. Stipule and stem were cut open. (The queen inside the previously sealed stem had crawled out of the internode. To indicate size relationships we did not remove her for the picture.)

*Scale insects.* Scale insects were found in 46% of the larger (more than 20 workers) *Camponotus macarangae* colonies in the primary forest (n = 13). The number of scale insects per tree was variable. The species was identified as *Coccus macarangae* (H. Heckroth, pers. comm.), a species frequently found in *Macaranga-Crematogaster* associations (unpubl. results).

In the association of *Crematogaster* with *M. lamellata*, 65% of the 30 plants studied contained coccids. *Coccus macarangae* was however quite rare. In the logged area, the most frequent species was a newly detected soft scale, *Coccus* sp. 84, which was abundant in Lambir and occurred in four other *Macaranga* species in the study area. Other coccids included *C. penangensis*, *C. secretus* and *C. tumuliferus*.

Young queens were never found with coccids during their fully claustral colony foundation in either *Camponotus* or *Crematogaster* associations. Coccids must therefore arrive later as crawlers by wind and get access to the colonies either actively and/or by the workers collecting and carrying them into the domatium.

## DISCUSSION

We conclude from our data that *Camponotus macarangae* is an obligate partner-ant of *Macaranga lamellata*. Besides being found in a high percentage of *M. lamellata* plants in the primary forest, the ability of queens to select, locate and colonize only specific hosts, and the details of plant handling by the workers, are strong evidence that this is a highly developed specific plant-ant. In addition, we found a second equally specialized partner-ant in *M. lamellata*, a *Crematogaster* morphospecies subgenus *Decacrema*. While the *Crematogaster* species was the only occupant found in the patch of logged forest, *Camponotus* was restricted to the primary forest where it was the common inhabitant of *M. lamellata*. The degree to which searching behavior of the young queens, or habitat preferences of the ants, determine this spatial pattern cannot be determined at the moment and further analysis of the distribution of the ant-colonists is clearly required. There is however some evidence from a different *Macaranga-Camponotus* association indicating that swarming *Camponotus* (subgenus *Colobopsis*) queens inhabiting *M.*

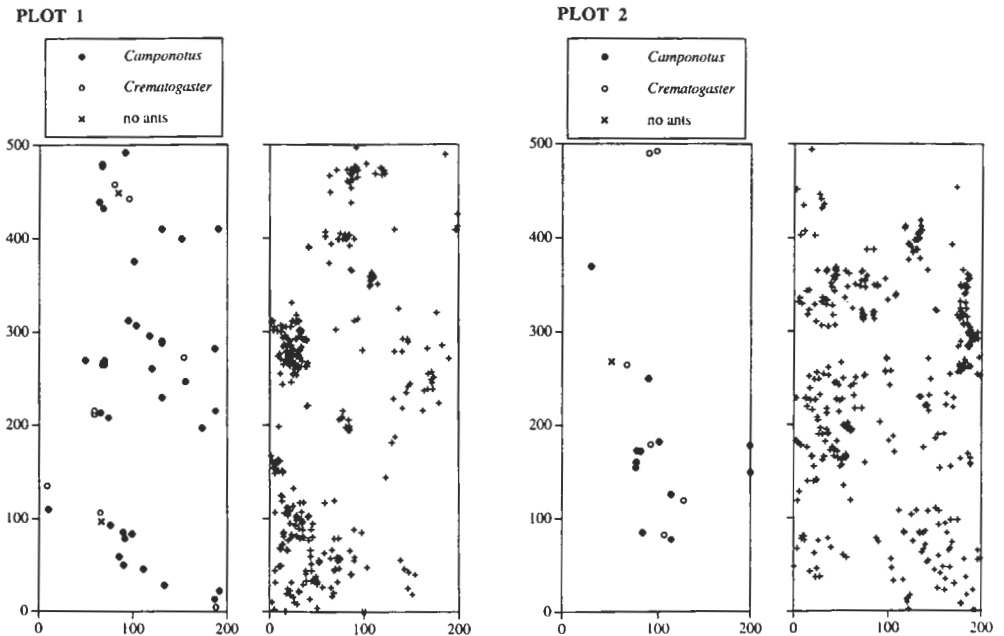


FIG. 4. Two 10-ha plots showing the spatial distribution of *Macaranga* individuals. Left graph shows spatial distribution of *M. lamellata* trees for which we identified the ant-colonist, and the right graph shows all other myrmecophytic *Macaranga* species in the same area. Plot scale in meters.

*puncticulata* avoid flying in open areas (Federle *et al.*, unpubl. results).

Not much information is available on the regular colonization of a single myrmecophytic plant species by different ant species. *Acacia* was reported with multiple *Pseudomyrmex* (e.g., Ward 1991) and *Cordia alliodora* with both *Azteca* and *Zacryptorcerus* (Wheeler 1942), without details on circumstances which can lead to a change in association. In Cameroon, myrmecophytic *Leonardoxa africana* (Caesalpiniaceae) is colonized by *Petalomyrmex phyllax* or *Cataulacus mckeyi*. *Cataulacus* is regarded as a parasite of the association without protective value for the plant and *Petalomyrmex* seems to be the superior competitor in high-light environments (McKey 1984). Other examples are *Clidemia heterophylla* and *Maieta guianensis* (Melastomataceae) from Peru, which are colonized by two specialized ants (Davidson *et al.* 1991). In this case, one ant species seems to replace the other only on fast-growing plants in sunny environments. Fonseca & Ganade (1996) report ant-plant interactions in the Neotropics to be highly asymmetrical: ant species in their study area often had fewer partners than plant species but they do not mention any myrmecophyte having two alternative specific partners. Most of the plants shared a set of ant species.

The most interesting myrmecophytic association for comparison with *Macaranga* is the Neotropical equivalent, *Cecropia* (Cecropiaceae). In the myrmecophytic *Cecropia*-complex all but one ant species can establish successfully on more than one host. Some of the symbiotic ants of *Cecropia* tend to be more strongly associated with habitats than with specific host plants (e.g., Davidson & Fisher 1991; Longino 1989, 1991; Yu & Davidson, submitted). The relative success of different ant species may differ in response to resource supply by the plants. For example, ants of the genus *Azteca* dominate on fast-growing hosts in sunny habitats, whereas only trees in shaded environments seem to be occupied by specialized ants from other genera (Davidson *et al.* 1989, 1991; Davidson & McKey 1993a, b). This holds true at least for *Cecropia pungara*, which is colonized by *Camponotus* sp. and *Pachycondyla* sp. Other gap *Cecropia* are dominated by *Azteca australis*, which tends to prefer hosts with especially high production of pearl bodies (Yu & Davidson, submitted). In distinct contrast, in *Macaranga* one *Crematogaster* species is usually more or less specifically associated with each host plant species (Fiala *et al.* 1994; Fiala

*et al.*, unpublished results). Despite the sympatric distribution of different *Macaranga-Crematogaster* associations on a small spatial scale, high ant-specificity is maintained, although a low level of overlap can exist in all species.

Both *M. lamellata* and its two specific partner-ant species seem to be highly evolved myrmecophytic organisms. How can their evolutionary development be understood? The plant shows all the characteristics of a highly developed myrmecophytic species of the *Macaranga* section *Pachystemon*, in which many of the species are myrmecophytes (Fiala & Maschwitz 1992a, b). With the exception of *M. lamellata* (and *M. puncticulata*, with unknown taxonomic affiliations) all myrmecophytic species of section *Pachystemon* are exclusively associated with species of *Crematogaster* subgenus *Decacrema*. This includes the *Decacrema* species sometimes associated with *M. lamellata*. These ants are very similar in all their myrmecological and behavioral characteristics, suggesting that they share a recent common evolutionary origin. Both the plant-inhabiting *Crematogaster* (subgenus *Decacrema*) and their *Macaranga* hosts (section *Pachystemon*) include numerous species, suggesting that one ancestral pair may have given rise to this diversity through cospeciation. Cladistic analyses of both ants and plants are necessary to test this hypothesis.

The role of coevolution in determining ant-plant associations is controversial. Davidson & McKey (1993a) discuss the evolutionary ecology of symbiotic ant-plant relationships in great detail, and suggest that host-switching, secondary colonization and ecological replacement are the predominant modes by which ant-plant associations are modified. However, the question remains as to how the second ant, *Camponotus macarangae*, could have got access to a myrmecophytic *Macaranga* section *Pachystemon* species. One possible scenario is that a subpopulation of *M. lamellata* might have lost its *Crematogaster* subgenus *Decacrema* partner-ant during an isolation event and a preadapted *Camponotus macarangae* ancestor locally took over both the highly developed myrmecophytic plant and the third partner group, the coccids. Slightly different ecological demands of the *M. lamellata*-ant species may then have prevented the displacement and extinction of one of the species. Our results from the logged forest suggest that *Camponotus macarangae* may prefer the primary forest environment but this needs to be verified in more study areas. It is interesting to note that *Coccus*

*macarangae* was found in *M. lamellata* with both *Camponotus* and *Crematogaster* ants. This coccid is not one of the common scale species found in myrmecophytic *Macaranga* species but with *Coccus secretus*, they are the only species which have so far been found on myrmecophytes other than *Macaranga* in Malaysia (H. Heckroth & A. Moog, Frankfurt, pers. comm.).

An alternative scenario for the origin of the *Camponotus-Macaranga* association is that *Camponotus macarangae* is the remnant of an ancestral form of *Macaranga* section *Pachystemon* ant-association. The association may then have been mostly taken over by the *Crematogaster* (subgenus *Decacrema*) ancestor, and become the basis for the radiation of this species-rich symbiotic complex. The primary and secondary associates are, however, difficult to distinguish. The latter scenario was favoured by Davidson & McKey (1993a), who speculate that aggressive ants of the genus *Crematogaster* have in general displaced prior ant-associates of host plants in South-east Asia, the prior ant-associates behaving as subordinates as in some subgenera of *Camponotus*. Support for this opinion could be the fact that *M. lamellata* secretes extrafloral nectar which, is the case only in one other myrmecophytic *Macaranga* species (*M. puncticulata*), which is also colonized by a (different) *Camponotus* sp. (Federle et al. 1994, see below). This could indicate an original association of *M. lamellata* by *Camponotus* ants.

Davidson and McKey's (1993a) opinion concerning *Macaranga* hosts in undisturbed forests has to be modified (p. 48: "Thus, *Macaranga* hosts in some undisturbed primary forests are occupied by a species with ... 11-segmented antennae, whereas hosts of forests and riverine edge typically contain any of an unrelated complex of species with ... and 10-merous antennae"). Our extensive sample size of the *Macaranga* species gives a different picture. The species referred to, growing in primary forest with a *Crematogaster* species with 11-segmented antennae, is the highly developed *M. winkleri*. It is always inhabited by a very specific *Crematogaster* species (our morphospecies #8, not in subgenus *Decacrema*) in primary forest and in heavily disturbed secondary habitats. *M. winkleri* also hosts a very specific coccid. *M. winkleri* is a species of high-light environments. It is included with one other species in section *Winklerianae* (Whitmore 1975). However the systematic position of the section is currently unclear. It is, though, superficially similar to *M. kingii* var. *pla-*

*typhylla* and *M. lamellata*, which can be regarded as primary forest species growing in shady understorey. *M. kingii* var. *platyphylla* was colonized mainly by a (*Decacrema*) *Crematogaster* sp. #3. This ant species occurred syntope with *Camponotus* and *Crematogaster* sp. #5 on *M. lamellata* in the primary forests, thus again demonstrating a high host-specificity.

The genus *Macaranga* also shows two other complexes of association which cannot be treated in detail here. Transitional species (Fiala & Maschwitz 1992 a, b) in which the ants are the typical *Crematogaster* subgenus *Decacrema* plant-ants, suggesting that the complex has evolved by host-plant switching, and species involved in a 2-partner association as in the *M. puncticulata*-complex (Fiala et al., in press). The above mentioned peat swamp forest species, *M. puncticulata*, found in Borneo and Peninsula Malaysia, is associated with a specific *Camponotus* species of the subgenus *Colobopsis* (*saundersi* species group). In this system the main food sources of the partner-ants are nectar and food bodies, and no trophobionts are tended (Federle et al. 1994; Fiala et al., unpubl. results). According to initial cladistic studies (Davies 1996, and unpublished results), and the distinct unspecific myrmecophytic character and habitat patterns (Fiala et al., in press), *M. caladiifolia* and *M. puncticulata* are probably not as closely related as was previously believed (Whitmore 1975).

The distinct myrmecophytic characteristics of these associations indicate their independent and possibly polyphyletic evolutionary development within the genus *Macaranga*, thus demonstrating the extraordinary diversity of ant-relations within this tree genus.

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## APPENDIX

Description of *Camponotus macarangae*,  
new species

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This new species belongs to the genus *Camponotus*. There are hundreds of described species in this genus therefore they cannot all be compared with the species inhabiting *Macaranga lamellata*. Under these circumstances a revision of the whole genus would be the optimal precondition for the description of new species. Such a revision, however, would be a lengthy task. To prevent *Camponotus* taxonomy from being blocked, we use the poorly-defined *Camponotus* subgenera of Emery (1925) for comparison. Furthermore, we have begun to define single distinct *Camponotus* taxa with respect to clear morphological and social biological characters (Dumpert 1985, Dumpert et al. 1989, 1995; Werner et al., in prep.). According to Emery (1925) 22 subgenera of this genus live in the Old World including Australia; 8 of these were found in the Indo-Malayan region. From these, *Camponotus macarangae* differs clearly. It is not as large as *Dinomyrmex*. The head is not flattened as in *Myrmoplatys*. In particular, *C. macarangae* is not associated with SE Asian myrmecophytic rattan palms like all known species of *Myrmoplatys* (Werner et al., in prep.). In contrast to *Colobopsis* *C. macarangae* is not dimorphic (no soldiers). It differs from *Karavaievia* *C. m.* it does not make silk nests and is also otherwise quite different from this morphologically distinct group (Dumpert 1985). In contrast to *Myrmotarsus*, *C. macarangae* has no compressed and hairy tibia. Workers of *C. macarangae* are not polymorphic as in *Myrmosaulus*, *Myrmamblys* and the subgenus *Camponotus*, and there are other important morphological differences as well.

Derivatio nominis: The species name is derived from the fact that this species was exclusively found in *Macaranga lamellata* plants.

Explanation of the abbreviations used below:

TL: total length. The total outstretched length of the individual from the mandibular apex to the gastral apex.

WL: Weber's length. The maximum length of alitrunk.

HL: head length. The straight-line distance between the anterior clypeal margin and the mid-point of the occipital margin in full-face view.

HW: head width. The maximum width of the head excluding the eyes.

CI: cephalic index =  $(HW \times 100)/HL$ .

SL: scapus length. The straight-line length of the antennal scape excluding the radicle.

SI: scapus index =  $(HW \times 100)/SL$ .

PW: pronotal width. The maximum width of the pronotum in dorsal view.

OD: ocular diameter. The maximum width of the eyes.

All measurements are in millimeters.

A. Holotype ♀: TL 3.9, WL 1.25, PW 0.64, HL 1.15, HW 1.02, CI 88.7, SL 0.82, SI 124, OD 0.25 or 0.24 HW

Head longer than wide (CI 88.7). HW nearly as large as the mandibles as near the occipital margin (Fig. 5a). Sides of the head weakly, occipital margin strongly rounded. Eyes are situated within the upper third of the head. Frontal carinae extend from the lower to the upper third of headlength. Apart from a slight indentation near the scapal insertion, the frontal carinae are straight. Clypeus not carinated and as long as wide (0.46 x 0.46 mm). Frontal area not visibly delimited and as much shiny as surroundings. Anterior clypeal margin considerably rounded. Mandibles short and slender, with lateral borders weakly curved and five unequal teeth on each masticatory border. The two apical teeth stronger than the remaining three. Antennal scapes relatively short, projecting beyond the occipital margin by about one fifth of their length. Apical flagellar segments slightly thickened.

Alitrunk with slight impression between promesonotum and propodeum. Pro- and mesonotum not marginated, propodeum rounded, showing neither margins nor thorns. Promesonotum, seen in profile, broadly rounded and higher than propodeum. Propodeal profile considerably flattened on top. Petiole with a broad base, tapering towards the apex into a blunt ridge. Seen from behind, petiolar apex is broad and notched.

Colour black to blackish brown. Mandibles, clypeus and the end of the gaster slightly lighter. Tarsi of the legs yellowish brown. Surface of head, alitrunk and gaster shiny. SEM-photograph reveals no special cuticular structures on head and alitrunk and only scarce decumbent pubescence (Fig. 5). Gaster with

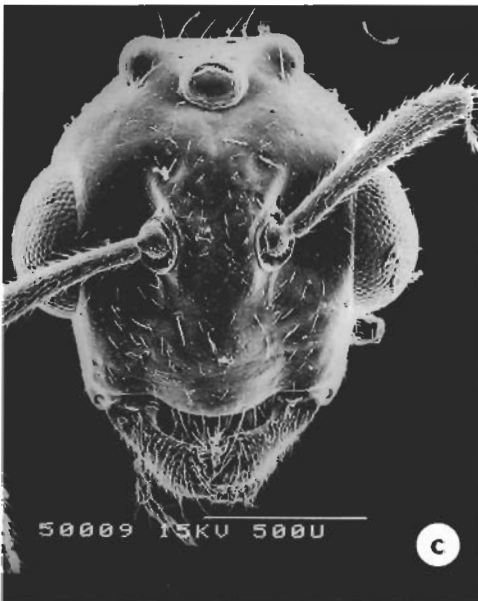
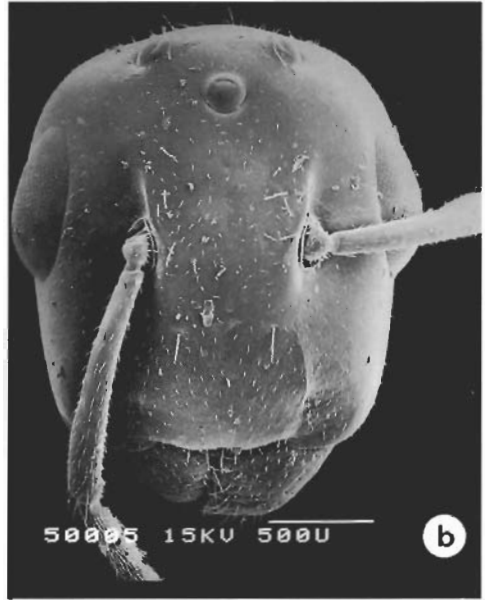
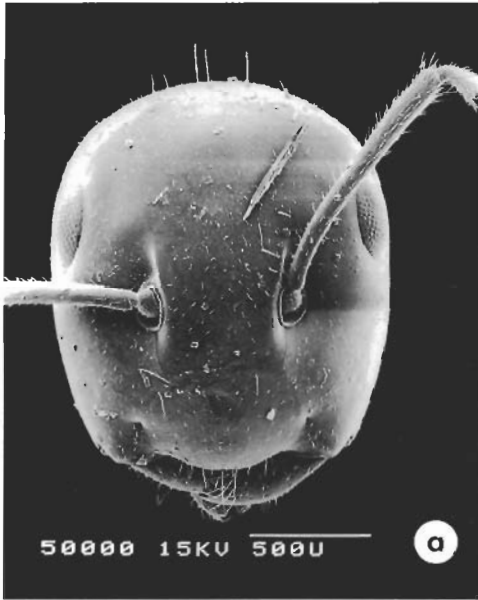


FIG 5. Scanning electron photographs of *Camponotus macatangae*; a) worker, b) queen c) male

Paratypes: TL  $3.7 + 0.25$  (standard deviation), WL  $1.23 + 0.1$ , PW  $0.7 + 0.045$ , HL  $1.1 + 0.1$ , HW  $0.99 + 0.08$ , CI  $90 + 1.2$ , SL  $0.78 + 0.07$ , SI  $125,1 + 7,5$ , OD  $0.25 + 0.02$  or  $0.24 + 0.05$  HW (measurements of 21 specimens)

Holotype: Borneo: Sarawak, Lambir-Park, living in *Macaranga lamellata*, Jan. 1994, U. Maschwitz leg. (Naturhistorisches Museum Basel)

Paratypes: 21 ♀ with same data as holotype and Borneo: Sarawak, Lambir-Park, living in *M. lamellata*, 9/22/1994, U. Maschwitz leg., and Borneo: Sarawak, Lambir-Park, living in *M. lamellata*, 2/2/1994, U. Maschwitz leg. (2 in Museum of Comparative Zoology at Harvard University; 2 in collection of the Forest Research Institute of Malaysia (FRIM) in Kepong; 2 in Museo Civico di Storia Naturale, Genova; 15 in collection of the author)

**B. Females:** Head considerably longer than wide (CI  $85 + 1.1$ ). Near the mandibles head nearly as wide as near the occipital margin (Fig. 5b). Sides of the head and occipital margin slightly convex. Eyes distinctly larger than those of workers and situated behind midlength of the sides of the head. Ocelli prominent, distance between ocelli 0.25 and 0.20 mm,

weak decumbent pubescence. Longer erect and sub-erect hairs especially on clypeus, but also on rest of head, alitrunk and gaster.

Workers of this species are monomorphic to a large extent: variations in size are very small.

respectively. Distance between ocelli and compound eyes 0.4 mm. Frontal carinae extend from the lower to the upper third of headlength. Apart from a slight indentation near the scapal insertion, they are straight and slightly divergent. Frontal area not visibly delimited and as much shining as surroundings. Clypeus not carinated and as long as wide (0.54 x 0.54 mm). Anterior clypeal margin nearly straight - only slightly convex - with small median excision. Mandibles strong, distinctly rounded on outside and with five unequal teeth on inside. The two apical teeth stronger than the remaining three. Antennal scapes relatively short, projecting beyond the occipital margin by about one fifth of their length. Apical flagellar segments slightly thickened. Petiole with a broad base, tapering toward the apex into a narrow ridge, when seen from the side. Seen from behind, the petiolar apex is broad and nearly straight, showing a very weak notch.

Whole body shiny, covered sparsely with fine decumbent pubescence. Longer erect and suberect hairs on whole body, especially on front parts of head and on mandibles. Head dark brown with lighter front parts and antennae, eyes black. Rest of body-yellow brown, legs darker.

Paratypes (9 ♂): TL 5.8 ± 0.35 (standard deviation), WL 2.05 ± 0.15, PW 1.15 ± 0.20, HI 1.42 ± 0.1, HW 1.2 ± 0.08, CI 85 ± 1.1, SL 0.97 ± 0.06, SI 123 ± 8, OD 0.52 ± 0.01 or 0.43 ± 0.05 HW

Paratypes: Borneo: Sarawak, Lambir-Park, living in *Macaranga lamellata*, Jan 1994, U. Maschwitz leg. and Borneo: Sarawak, Lambir-Park, living in *M. lamellata*, 9/22/1994, U. Maschwitz leg., and Borneo: Sarawak, Lambir-Park, living in *M. lamellata*, 2/2/1994, U. Maschwitz leg. (2 in Museum of Comparative Zoology at Harvard University; 2 in collection of the Forest Research Institute of Malaysia (FRIM) in Kepong; 2 in Museo Civico di Storia Naturale, Genova; 3 in collection of the author)

**C. Males:** Head with nearly parallel sides (not trapezoidal) and distinctly longer than wide (CI 87.4). Eyes prominent, extending to the upper end of head sides. Occipital margin strongly convex with protruding ocelli (Fig. 5c). Clypeus broad (width 0.27 mm) and weakly delimited from surrounding head parts. Anterior clypeal margin rounded (convex). Short frontal carinae divergent, reaching back to upper third of head. Eyes very large: maximum diameter 0.38 mm or 0.5 HW. Mandibles strong and

weakly rounded on the outside; inside armed with four teeth, one strong apical and three subequal rounded ones. Scapes short, projecting only slightly beyond occipital margin of head. Pedicel expanded at its distal end and thicker than following flagellar segments. Apical flagellar segments not thickened. Petiolar scale triangular in profile, with a broad base tapering to a blunt ridge. Ridge with a deep median excision.

Whole body shiny. Head in most parts brown, mandibles and front parts of head - as well as antennae - yellow-brown. Rest of body, including legs, yellow to yellow-brown. Wings whitish with yellow veins. Decumbent pubescence sparse on whole body; higher erect and suberect hairs denser, especially on head and alitrunk.

Paratypes (9 ♂): TL 4.2 ± 0.35 (standard deviation), WL 1.75 ± 0.15, PW 0.88 ± 0.15, HI 0.84 ± 0.04, HW 0.75 ± 0.03, CI 88.9 ± 3.5, SL 0.6 ± 0.05, SI 131.6 ± 9.5, OD 0.37 ± 0.01 or 0.46 ± 0.05 HW or 0.51 ± 0.02 HW

Paratypes: Borneo: Sarawak, Lambir-Park, living in *Macaranga lamellata*, Jan 1994, U. Maschwitz leg. and Borneo: Sarawak, Lambir-Park, living in *M. lamellata*, 9/22/1994, U. Maschwitz leg., and Borneo: Sarawak, Lambir-Park, living in *M. lamellata*, 2/2/1994, U. Maschwitz leg. (2 in Museum of Comparative Zoology at Harvard University; 2 in collection of the Forest Research Institute of Malaysia (FRIM) in Kepong; 2 in Museo Civico di Storia Naturale, Genova; 3 in collection of the author)

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