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Two new myrmecophytic associations from the Malay Peninsula: ants of the genus *Cladomyrma* (Formicidae, Camponotinae) as partners of *Saraca thaipingensis* (Caesalpiniaceae) and *Crypteronia griffithii* (Crypteroniaceae)

1. Colony foundation and acquisition of trophobionts

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Summary

In Peninsular Malaysia the trees *Saraca thaipingensis* (Caesalpiniaceae) and *Crypteronia griffithii* (Crypteroniaceae) are inhabited by ants. In the vicinity of Gombak, near Kuala Lumpur, the hollow internodes of young *Saraca thaipingensis* plants are colonized mainly by two *Cladomyrma* species. In larger trees a *Crematogaster* sp. is also found. *Crypteronia griffithii* is inhabited by a third species of *Cladomyrma*. None of these species is conspecific with any of the three *Cladomyrma* taxa so far described. The colonies are founded by single mated queens, which have a conspicuous, sphecid wasp-like behaviour when searching for host plants and nest sites. They chew holes into the plant internodes and hollow them out to provide nest sites. Coccids and pseudococcids are cultivated within the internodes. The homopterans are not carried by queens on their nuptial flights. They apparently find their way by themselves into the cavities or are perhaps carried there by the worker ants. The *Cladomyrma* ants on *Crypteronia* are not aggressive, in contrast to those on *Saraca thaipingensis*.

The relationship of *Crypteronia* with ants seems to be obligatory, whereas *Saraca* was only partly colonized by *Cladomyrma*. The interaction of *Saraca* with *Crematogaster* sp. is loose and facultative, since the *Crematogaster* sp. also lives on other t ree species. Our studies have now revealed four *Cladomyrma* spp. which are regularly associated with plants. The genus therefore seems to have an entirely myrmecophytic way of life.

Introduction

To date, several species of the tree genus *Macaranga* (Euphorbiaceae) and three genera of rattan palms from the Malay Peninsula have been identified as myr-

mecophytic plants (Ong, 1973; Soepadmo, 1978; Tho, 1978). They are associated with ants of the genera *Crematogaster* and *Camponotus*, respectively. During our investigations of Malaysian myrmecophytes we encountered two more tree species that have not been previously reported to be ant-plants, namely: *Saraca thaipingensis* (Caesalpiniaceae) and *Crypteronia griffithii* (Crypteroniaceae). They are inhabited by different species of the camponotine genus *Cladomyrma*. Information about this genus is scarce, and its biology is largely unknown. *Cladomyrma* was reported to have been found in the internodes of a Bornean shrub (by Hewitt, in Wheeler, 1910). Wheeler thought that *Aphomomyrmex hewitti* (= *Cladomyrma hewitti;* Chapman and Capco, 1951) was "a timid tree ant, which habitually nests in small colonies in vegetable cavities". In Sumatra, Roepke (1930) observed queens of an ant species obligatorily carrying homopteran plant lice in their jaws during their nuptial flights. This species was presumed to belong in *Cladomyrma*, because it possessed eight-jointed antennae. We present here results of life history studies on this little known genus, mainly concerning colony foundation and the acquisition of homopterous trophobionts.

Materials and methods

Field observations were carried out during a six month's stay (September 1988–March 1989) in Peninsular Malaysia. More than 70 trees of *S. thaipingensis* and *C. griffithii* were censused for ant colonization. Branches were thoroughly dissected in order to study colony structure. *S. thaipingensis* was studied mainly in the Gombak Valley 40 km NE of Kuala Lumpur (250 m a.s.l.), and in the hill regions of the Genting Highlands (500–900 m a.s.l.). Fifteen trees were investigated also in Templer Park (Selangor, 20 km N of Kuala Lumpur) and near Tapah (Selangor). *C. griffithii* was studied in various parts of the Malay Peninsula: Gombak Valley, Templer Park, Bukit Renggit Forest Reserve (near Bentong, Pahang), Maxwell Hills (near Taiping, Perak) and Pasoh Forest Reserve (near Kuala Pilah, Negri Sembilan). A second species of *Crypteronia*, *C. paniculata*, was also studied; four specimens only were found on Penang Island. Voucher specimens of the *Cladomyrma* ants are deposited at the British Museum (Natural History), London.

Results

a) Ant occupants of Saraca thaipingensis: General observations

Saraca is a common tree in stream valleys, along rocky banks near the headwaters. *S. thaipingensis*, with its large pinnate leaves, is the most common representative of the genus. The leaf buds develop rapidly into a tassel of purple, limp new leaves, which dangle for several days before stiffening and straightening. The margins at the base of each leaflet carry up to nine extrafloral nectaries. *S. thaipingensis* was frequently found by us to be inhabited by various ants. In the Gombak Valley and other nearby valleys of the Genting Highlands, *Saraca* trees were often inhabited by

two *Cladomyrma* species: one common and one relatively rare species. They are morphologically quite distinct, especially the queens (light yellow-brown in species A; blackish in sp. B).

A *Crematogaster* species also lived in the hollow internodes of the trees, as did various so-far unidentified ants of different subfamilies. Larger trees were often inhabited by huge colonies either of *Cladomyrma* or *Crematogaster* sp.

After shaking or other disturbance of the host plants, workers from large colonies of both species quickly left the interior of the stem and attacked fiercely, by biting and releasing defensive secretions. In the internodes, which were hollowed out for lengths of up to several meters, we found ant brood, and several species of coccids and of one pseudococcid. Twice, as stems were being cut and opened, we observed *Cladomyrma* workers carrying small pseudococcids. After thorough search, we also found pseudococcids on the surfaces of young shoots under bud bracts.

On new, young shoots growing from the stumps of felled trees we observed all stages of colony founding of both *Cladomyrma* spp. but not of the *Crematogaster* sp., which occurred only on larger trees. In the latter we saw workers biting large, irregular holes into internodes and leaf bases. The *Crematogaster* workers found on *Saraca* did not live there exclusively, but were typically found also on other tree species in the vicinity.

Cladomyrma sp. A and B: Nest- and colony-structure

In Gombak Valley and Genting Highlands we checked 40 young branches of *Saraca thaipingensis* for ant-occupation. About a third of them were colonized by queens of *Cladomyrma*. Branches up to 1.8 m in length contained up to six colony founding queens.

The nest cavities were 1.5–5 cm long. The large entrance hole chewed by the founding queen closes quickly due to growth of the plant, except for a small slit, which is kept open by the queen. This is too small even for the passage of small workers. Up to 9 additional, very narrow slits were also present in founding nests. These were opened and maintained by the resident queens. Pseudococcids were observed at the inner openings of some of these slits.

Table 1 shows the results of the survey. Many dead queens were found in the nests. These could be easily located from outside since the entrance holes of their nest cavities had usually been closed by the growing bark of the host plant. It can be seen from the table that all newly founded colonies which lacked eggs also did not possess any trophobiotic pseudococcids. With increasing size and age more and more colonies had trophobionts.

We closely followed the progress of colony development by three queens of *Cladomyrma* sp. A by opening their nest chambers several weeks after foundation. During the excavation and closing of their nest cavity these females had no associated pseudococcids. After 62 days we found seven workers, much brood and four pseudococcids of different sizes in the internode with queen 1. In the internode with queen 2, after 72 days there were three workers, a small amount of brood and two medium-sized pseudococcids. Queen 3 had six workers, brood and several coccids after 106 days.

Queen searching behaviour for nest sites and colony foundation

We observed alate females of both *Cladomyrma* spp. searching for a suitable host tree and nest site on four occasions. All of them (3 of *Cladomyrma* sp. A and 1 of *Cladomyrma* sp. B) were observed on dry, sunny days, at times between late morning and late afternoon. Their behaviour was very conspicuous and unusual for female ants. They landed accurately on the thin twigs of *Saraca* trees and ran about quickly, in a manner resembling that of searching sphecid wasps. They appeared to check the twigs. If these were obviously not suitable for colonization because of age, or were already inhabited, the queens moved to another plant. We observed three other females of *Cladomyrma* sp. A that had already shed their wings and were wandering on the twigs (between 12 a.m. and 3 p.m.). They were apparently searching for young internodes and also were seen attempting to enter already occupied internodes, but these were defendend by the inhabiting ants. We captured one queen of species B to check whether she carried pseudococcids in her mandibles, but she did not.

Construction of the nest cavity

Nine further females were observed while constructing their nest cavities (Fig. 1). There were no perceived behavioural differences between the two species. Following is a short description of the process: A queen of *Cladomyrma* sp. A had tried vainly to intrude into an already occupied internode. She was then placed by the observer onto a suitable young internode where she immediately systematically patrolled the youngest internodes and leaves. Within 10 min she began to chew a hole into a soft internode. 30 min later a longish hole had been bitten along the twig through the woody part of the stem. The queen continued without pause, and after nother 80 min, a cavity in the pith, which was large enough to shelter the ant, had been prepared. The queen immediately disappeared into this space. During the excavation process she continually changed her position. The excavated material was removed in large portions and ejected from the bore-hole in batches of one to three small pieces. Coming to the surface, the queen turned around, and then pushed the material beneath her body, working it backwards, between the legs. We observed this excavation behaviour in seven females of species A and two females of species B.

We never found pseudococcids near the entrance holes of initial excavations. All queens retreated into the hole as soon as this was sufficiently large. They continued excavating the interior. They pushed out the pith from inside and largely closed the hole in this way. The process of chewing the hole took from 120 to 230 min. One of the queens was disturbed by other ants during the process: she first hid under a leaf and then started to bite at another site. Five of the freshly colonized internodes opened after one day contained no pseudococcids.

b) Ant occupants of Crypteronia: Cladomyrma sp. C

Crypteronia contains only four species worldwide; two are present in Malaysia. The young leaves have a striking bluish colour. Of 50 *C. griffithii* trees which were

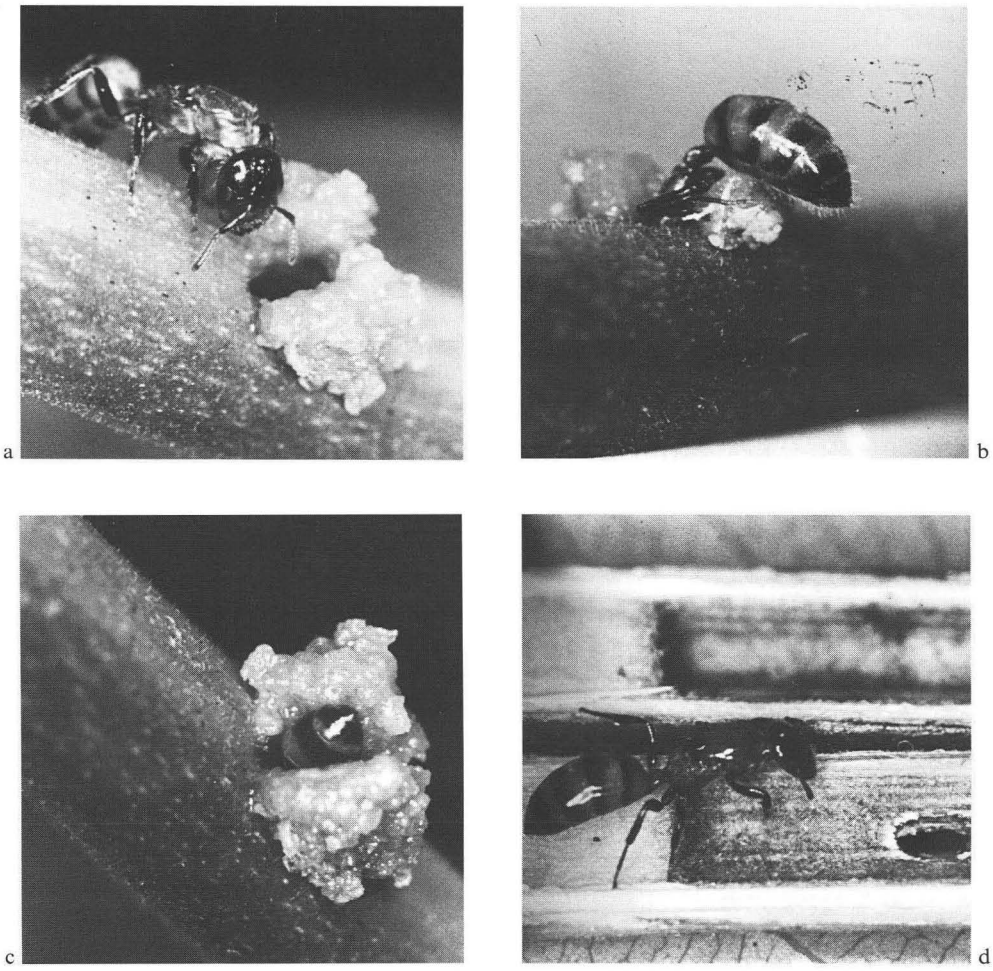

Figure 1. Construction of the nest cavity in *Saraca thaipingensis* by a colony-founding queen of *Cladomyrma* sp. A. Different stages from start of chewing to finished entrance hole. Finally the queen will largely close the entrance with pith (d: view at the interior of an opened branch)

checked, 45 were occupied by a small *Cladomyrma* species with yellow workers, which were found both day and night on the surface of young leaf flushes, where they moved about and gnawed entrance holes into new internodes. Workers were not as a rule aggressive. The branches of *C. griffithii* were hollowed out by the ants for a length of several meters, and internodal septa were also removed. The internodes contained brood, a pseudococcid species and one coccid species. Two large trees were completely uninhabited by ants, although in the vicinity small trees were colonized.

On young trees and new shoots of cut trees we found eleven living colony-founding queens, and seven dead females. The entrance holes of their nests were kept

Table 1. Pseudococcids in nest chambers of colony founding queens of *Cladomyrma* sp. A and B in *Saraca thaipingensis*

Species	Number of queens (with pseudococcids)					
	Dead	Living				
		Without eggs	With eggs	With brood	With brood and workers	Total
sp. A	?	3(−)	10(2)	9(9)	5(5)	27(16)
sp. B	?	3(−)	1(1)	1(−)	1(1)	6(2)
sp. A + sp. B	24(5)	6(−)	11(3)	10(9)	6(5)	33(17)
Percentage of living pseudococcids in sp. A + sp. B (+ dead)	13 (+8)	–	27	90	100	55

open as small slits. Nine of these queens had pseudococcids, one had brood but no pseudococcids, and another had brood, along with a few workers.

Slits additional to the entrance holes in these nests were not observed. They thus contrast with nests of the *Cladomyrma* species observed on *Saraca*.

We observed one colony-founding queen around 4 p.m. She was still winged, and behaved similarly to a sphecid wasp, like other *Cladomyrma* species reported above from *Saraca*. She patrolled an already occupied internode, and did not carry pseudococcids. Later dissection showed that she had been mated, and that her spermatheca was densely filled with sperm. All four specimens of *Crypteronia paniculata* found on Penang Island, and another at Ulu Gombak were not inhabited by ants.

Discussion

Saraca thaipingensis is a common tree along riverbanks in primary forest. Flowers as well as leaf flushes are fed upon by a number of herbivores. We observed chrysomelid beetles, weevils and various butterflies and moths (see Fiedler and Maschwitz, 1989). Ants are also common on *Saraca*, where they visit extrafloral nectaries or trophobionts. Some nest in abandoned cavities excavated by stem-boring caterpillars. In the Gombak Valley we observed only *Cladomyrma* spp. and *Crematogaster* sp. excavating the internodes actively. The workers of *Crematogaster* produced larger, more irregular holes. We found neither colony-founding queens of this species, nor mated females in intact colonies. We do not know how their symbiotic homopterans are acquired. *Crematogaster* sp. workers also nested on neighbouring trees of other plant species, from which they foraged on *Saraca* plants. Therefore the association of *Saraca* with *Crematogaster* sp. seems to be loose and facultative.

This is not the case in the association of *Saraca* with the two *Cladomyrma* species. Several factors indicate an obligatory relationship as far as the ants are concerned.

These include the striking and atypical host plant locating behaviour, search for nest sites, and the quick and effective excavation of nest cavities by founding queens. Moreover, we never found the ants away from *S. thaipingensis* plants, although we searched for them intensively. Other *Saraca* species in Peninsular Malaysia have not yet been investigated. In Borneo, near Poring, Sabah, we checked 15 *Saraca declinata* trees. They were not inhabited by *Cladomyrma* ants.

The question as to how the trophobionts get into the ant-association is important. The most common pseudococcid species discussed here does not live only in the hollow internodes, as do some, at least, of the coccids found in myrmecophytic *Macaranga* species (Tho, 1978; Fiala et al., 1989). It was also found on the surface of the host plants. Nothing is known at present concerning its taxonomic position. The ant species discussed by Roepke (1930) as a probable *Cladomyrma* sp. was reported to carry homopterans regularly on its nuptial flight. Unfortunately, nothing more is known about the biology of this ant. Roepke invoked the 8-jointed antenna in identifying his ants as *Cladomyrma*. According to Agosti (pers. comm.), this character is not very taxonomically definite here, so it is therefore possible that Roepke's ants could have represented another genus, for example *Acropyga*, which is known to carry homopterans during its nuptial flight (Bünzli, 1935; Buschinger et al., 1987).

Schremmer (1984) assumed the carrying of scales also for the *Pseudomyrmex* partners of *Triplaris* in South-America. However, he never directly observed such behaviour. We have found that *Crematogaster* ants in *Macaranga* do not carry homopterans with them on their nuptial flights (Fiala and Maschwitz, 1990). The same seems to be true for the *Cladomyrma* species on *Saraca*. We never found pseudococcids during nest construction or in freshly founded colonies. One winged queen of *Cladomyrma* that had just arrived on a host plant had no pseudococcids with her. With increasing age the percentage of homopteran-inhabited nests gradually increases. 1.5 to 3 months after colony foundation pseudococcids were present beside brood and workers, indicating that they must have arrived later than the time of nest establishment. Other observations support this assumption; for example, we observed tiny pseudococcids of early developmental stages abroad on the *Saraca* plants. They are able to pass through the narrow entrance slit kept open by the queen and those excavated later. These may therefore be considered to be entrances constructed for use by the trophobionts, enabling them to enter the nests easily. Perhaps they are later also transported into the nests by the workers. The females chewed rapidly and continuously, without ever leaving the hole under excavation. They disappeared immediately into their chambers when the holes had reached a suitable size, and closed the entrance usually with pith material. The continuation of work in the narrow, wet nest chambers would seem to preclude the immediate cultivation of young pseudococcids. The association of *Crematogaster* and its trophobionts may originate in a similar way as in *Cladomyrma*. In the Gombak Valley many *Saraca* trees were colonized by *Cladomyrma* spp. We never found occupied specimens in other areas.

Compared to *Saraca* the association of *Cladomyrma* with *Crypteronia griffithii* seems to be obligatory. We found this tree species in various parts of the Malay Peninsula, and almost without exception it was observed to be associated with

Cladomyrma. Our results indicate that pseudococcids are not transported during the nuptial flight and colony foundation in this association.

Larger colonies of *Crematogaster* sp. as well as *those of Cladomyrma* spp. on *Saraca* are very aggressive and probably protect the trees against herbivores. Thus far, there is no direct support for this hypothesis, but it is likely that the ant inhabitants have a function similar to that of *Crematogaster borneensis* ants living in *Macaranga* trees (Fiala et al., 1989). We plan to investigate this aspect more thoroughly in later work.

Taxonomic position of Cladomyrma

At present the genus *Cladomyrma* contains only three named species, all described from Borneo (Emery, 1894; Wheeler, 1910; Donisthorpe, 1937). Two of them are known only from queens, and nothing is known about their habitat preferences of life histories. Our specimens of ant species from *Saraca* and *Crypteronia* were identified as representatives of undescribed species of *Cladomyrma* (Bolton, in litt.). A revision of the genus is planned.

Interestingly, *Cladomyrma* seems to be closely related to two other myrmecophytic ant genera, *Petalomyrmex* and *Aphomomyrmex*. *Petalomyrmex phylax* (an associate of the tree *Leonardoxa africana*) was described as a new monotypic genus closely related to *Aphomomyrmex* (McKey, 1984). *Aphomomyrmex* also appears to be monotypic; the sole species, *A. afer*, is a widespread but apparently rare arboricolous ant in the central African forest zone (Snelling, 1979). This species has been recorded living in *Leonardoxa letouzeyi* (McKey, 1989).

In Sabah (Borneo) we discovered another association between a *Cladomyrma* species and a plant: the woody climber *Millettia nieuwenhuisii* (Fabaceae) (Maschwitz et al., 1989). Our studies have now revealed a total of four *Cladomyrma* spp. associated with plants. They are active colonizers of trees and climbers. *Cladomyrma* thus seems very likely to be a genus which has an exclusively myrmecophytic way of live.

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