

THE ARACHNE-GROUP OF POLYRHACHIS
(FORMICIDAE, FORMICINAE) :
WEAVER ANTS CULTIVATING HOMOPTERA ON BAMBOO
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Reçu le 19 janvier 1989

Accepté le 25 avril 1989

SUMMARY

The biology of two species of *Polyrhachis* which together form the *arachne* species-group is described. Both *Polyrhachis arachne* Emery 1896 and *Polyrhachis hodgsoni* Forel 1902 are confined to broad-leaved species of bamboo, but there is no ant-plant mutualism. They collect Homoptera on bamboo plants and cultivate them in leaf pavilions. The evolutionary advantages of this type of ecological specialization are discussed.

ZUSAMMENFASSUNG

Die *arachne*-Artengruppe der Gattung *Polyrhachis* (Formicidae, Formicineae) :
Webeameisen, die Homopteren auf Bambus kultivieren

Die Biologie zweier *Polyrhachis*-Arten, die die *Arachne*-Artengruppe bilden, wird beschrieben. *Polyrhachis arachne* EMERY 1896 und *Polyrhachis hodgsoni* FOREL 1902 sind auf das Leben auf breitblättrigen Bambusarten spezialisiert, ohne jedoch mit diesen in mutualistischer Symbiose zu leben. Sie tragen verschiedene Homoptera in Blattpavillons und halten sie dort. Die evolutiven Vorteile dieser Einnischung werden diskutiert.

INTRODUCTION

Polyrhachis is one of the largest genera of ants. Most species are arboreal and weave their nests with larval silk. Nevertheless *Polyrhachis* species are highly variable in many other aspects of their biology, e.g., in their mode of colony foundation, in colony size, recruitment behaviour (DOROW and MASCHWITZ in prep.).

During our comparative studies on the systematics and behavioural ecology of this genus we observed two species which have rather unusual life habits: they are restricted to bamboo plants as habitat and live in a tight trophobiosis with homopterans which they cultivate in silk pavilions. The two species, *Polyrhachis arachne* Emery 1896 and *Polyrhachis hodgsoni* FOREL 1902, form the *arachne* species-group. They belong to the subgenus *Myrmhophla*, which is characterized by a lack of margination on the sides of the thorax and by spines on thorax and petiole (a revision of the subgenus is in preparation by the senior author). Both species have hooklike spines on the propodeum. The gaster of *P. arachne* is smooth and shiny black, that of *P. hodgsoni* dull and somewhat pubescent.

Little is known about the distribution of the two species. Very few geographic records are given in the literature; a few more have been added after our identification of hitherto undetermined museum material. *P. arachne* is now known from Burma: Karen Hills, Tenasserim; Ruby Mines, Upper Burma; Shan States; Thailand: Bandon; Malaysia: Tapah Mountains, Perak; Kepong, Selangor; Ulu Gombak, Selangor; Genting Highlands, Selangor; Indonesia: Panti, Sumatra; Buitenzorg, Java; Palabuan, Java (Holotype) (ANDRE, 1896; BINGHAM, 1903; EMERY, 1896; FOREL, 1911; KARAVALEV, 1928).

P. hodgsoni had been known only from Burma: Moulmain (Holotype); Yunzalin River, Tenasserim; Papun (BINGHAM, 1903; FOREL, 1902), until we found it in Malaysia: Ulu Gombak, Selangor.

MATERIALS AND METHODS

We studied 18 colonies of *P. arachne* and 6 of *P. hodgsoni* in West Malaysia. For evaluating the colony structure, nests and pavilions were put into plastic bags and the ants were narcotized with Enfluran. After censusing the ants were released at their original nest plant where the colonies soon resettled. Because the ants are polydomous it was impossible in many cases to determine whether or not a whole colony had been collected. But for each species at least one isolated colony could be censused completely.

RESULTS

Plant specificity

We collected several hundreds of nests of *Polyrhachis* species, mostly on various trees and shrubs, including palms and ginger plants, which highly resemble bamboo in leaf shape, but we never observed any kind of plant specificity in a *Polyrhachis* species except in the *arachne*-group, where the two species were restricted to broad-leaved species of bamboo (*Gigantochloa scortechinii* Gamble 1896, *Schizostachyum* sp.).

1.) *Polyrhachis arachne* Emery 1896**Nest**

P. arachne nested in bamboo culms with inner diameters of 1.4-4 cm (median = 1.6 cm, $\bar{\phi}$ = 2 cm, SD = 1.1 cm, n = 10), with no regard to whether the culms were living or dead or whether they were in a vertical or in a horizontal position. The ants avoided culms lying directly on the ground. Nests were 33.5-90 cm long (median = 61.5, $\bar{\phi}$ = 61.6 cm, SD = 23.1 cm). We found nests 60-230 cm above the ground. As entrances the ants used preformed holes, e.g., those made by woodpeckers or the openings of broken stems. The entrance openings were narrowed to 2-3 mm in diameter by silk, which in addition was covered with a detritus layer on the outside. A single nest had 1-4 entrances. These nests were generally confined to one internode each as the ants were unable to perforate the nodes. If several internodes of one culm had preformed holes, all of them could be occupied.

The inner surface of the bamboo nest wall was lined with a very thin layer of silk to which larvae and pupae were attached longitudinally by a few threads of silk. At the bottom of these nests sometimes a lot of detritus had accumulated, mainly remains of insect prey (beetle elytra, head capsules of cerambycid larvae, ootheca of cockroaches, and unidentified arthropod remains).

Each of the 2-4 partial nests found per colony (n = 10) contained 33-340 workers (median = 136, $\bar{\phi}$ = 165.7, SD = 109.7), 14-35 pupae (median = 27, $\bar{\phi}$ = 30.3, SD = 17.6), 3-11 larvae (median = 5, $\bar{\phi}$ = 6, SD = 3.6), no alate sexuals and varying numbers of eggs. Only rarely a larva or some offered pieces of food were transported from nest to nest or from pavilion to nest. Judging from the fact that there was no permanent worker traffic between the partial nests, they seemed to be relatively autonomous, but shared the same foraging area. The one colony which was collected as a whole was monogynous and its queen was found in one of the nests described above.

Pavilions

While nests are considered as places for rearing the brood and housing the queen, pavilions are accessory structures for keeping trophobionts. The main food source of *P. arachne* was honeydew from homopterans that were kept inside silk pavilions. Though many large leaves of different kinds of plants were available, the ants built their pavilions almost exclusively beneath the leaves of bamboo. Among hundreds of pavilions, only one was found below a ginger leaf that had direct contact with bamboo leaves. No Homoptera were found inside this pavilion. Up to 6 pavilions were clustered at one branch (fig. 1). No favoured height or compass direction could be detected, but there were no pavilions in the dark inner area of the bamboo



Fig. 1. — Pavilions of *Polyrhachis arachne* below bamboo leaves.

Abb. 1. — Pavillons von *Polyrhachis arachne* unter Bambusblättern.

grove, possibly due to insufficient insolation. The pavilions were found 1-15 m above ground. They were built with webs of larval silk. The silk subsequently was covered with coarse detritus particles on the outside of the pavilion such as dry material from the leaves or stems of bamboo or pieces of decaying wood. Individual particles were up to 3 cm long. The silk web was normally woven rather crudely so that the ants could escape at many sites of the pavilion when disturbed. In addition 1-2 distinct entrances were present at variable sites.

Pavilions normally covered the whole or nearly the whole width of the leaf and about 2/3 of its length. They were 4.5-25.0 cm long (median = 11 cm, $\sigma = 11.4$ cm, SD = 4.8 cm) and 1.6-7.0 cm wide (median = 4 cm, $\sigma = 3.7$ cm, SD = 1.2 cm) ($n = 59$). Besides this normal type, pavilions were also built between two leaves. In one unusual case we observed a pavilion constructed around the stem of a young bamboo at the site, where the small branches inserted.

Workers numbered from 3-174 per pavilion (median = 32.5, $\sigma = 48.5$, SD = 39.4, $n = 22$). Alate sexuals were found only rarely and in low numbers (females: median = 0, $\sigma = 0.1$, SD = 0.4; males: median = 0, $\sigma = 0.1$, SD = 0.3; $n = 31$). Pupae numbered from 0-32 per pavilion (median = 0, $\sigma = 8.4$, $s = 9.1$), large or medium sized larvae from 0-8 per pavilion (median = 0, $\sigma = 1.6$, SD = 2.3). About 40 % of the pavilions contained no pupae and 20 % no larger larvae. Small larvae, which sometimes occurred in large numbers, and eggs were not counted.

The area controlled by one colony could comprise several clumps of bamboo. Some of these were separated by low vegetation which was traversed by the workers. The areas of 3 isolated colonies were measured (distances refer to the maximum diameters of the crown regions): A: 15 m \times 4 m, (20 pavilions, two of them occupied by other ants, 5 of them empty); B: 18 m \times 4 m, (23 pavilions, 3 nests); C: 1. clump: 3.50 m \times 3.50 m, 2. clump: 5.00 m \times 5.00 m, 3. clump: 6.00 m \times 6.00 m (13 pavilions, one of them occupied by other ants, 2 nests). Colony C was censused completely. It contained 1176 workers, 1 queen, and no alate sexuals. Compared with other-not fully censused-colonies, this seemed to be a relatively small one. *P. arachne* and *P. hodgsoni* are only active during daytime. To avoid underestimation of the number of workers by missing the foraging specimens, we collected nests and pavilions after dusk at which time most individuals could be expected inside the pavilions or nests.

Weaving behaviour

Weaving was carried out by a worker which held a last-instar larva by its neck constantly antennating the sides of the larva's head and waving the larva to-and-fro (see fig. 2: *P. hodgsoni* with the same behaviour). The larva supported this movement by stretching its head in the direction of the movement. By tipping the head of the larva to the leaf or the previously built part of the pavilion the silk thread was fixed in place. In this way



Fig. 2. — Weaving larva of *Polyrhachis hodgsoni*.

Abb. 2. — Webende Larve von *Polyrhachis hodgsoni*.

about 7.5 mm were spanned. By successively adding new threads of silk the ants were able to build large webs. Other workers brought plant particles and attached them to the outside of the fresh silk web. Silk from destroyed pavilions was rolled to balls larger than the ant's gaster and reused for pavilion building. Sometimes relatively short pavilions were built which were later enlarged without full removal of the former outer walls. So a few of the pavilions were divided into two to several more or less separated compartments.

The underside of the leaf constituting the upper wall of the pavilion was covered with a very thin layer of silk fixed to the numerous small hairs of the bamboo leaf. It was completely free of detritus. The brood was fixed longitudinally to this layer with a few threads of silk. In some of the pavilions refuse piles were found near the leaf tip.

Trophobiosis

The pavilions contained Hormaphididae and Pseudococcidae. At least two species of each taxon were involved, which have not been identified so far. Nearly all pavilions inhabited by the ants contained homopterans. Species of Hormaphididae and Pseudococcidae were often found together in the same pavilion. Pseudococcidae were present in all pavilions which contained trophobionts (2-300, median = 33, $\sigma = 81.5$, SD = 96.0, $n = 12$), and they outnumbered the aphids, which occurred only in 30-75 % of a colony's pavilions (0-150, median = 0, $\sigma = 21.6$, SD = 44.1, $n = 19$). The total numbers of homopterans varied from 0 to 370 individuals per pavilion (median = 104, $\sigma = 122.8$, SD = 113.5, $n = 24$). The nests normally contained no homopterans. Only in one nest in a green bamboo culm there were 4 Pseudococcidae tended. *P. arachne* workers collected all honeydew-producing homopterans they encountered on the bamboo and carried them into the pavilions. No homopterans were present outside the pavilions unless strongly protected by other ants (e.g., by *Crematogaster*, *Myrmicaria*). Eggs of homopterans were found on the bamboo leaves, even on those where pavilions were built. For evaluating the trophobiont-retrieving behaviour in more detail, we presented to *P. arachne* workers Hormaphididae and Pseudococcidae from destroyed pavilions of their own or of foreign colonies. Soon the workers accumulated at such sites by recruitment behaviour and cautiously started to pull at the aphids and pseudococcids. When these released their grips, they were carried to a pavilion, normally to the nearest one, but sometimes also more than 5 m away. Occasionally workers handed the homopterans over to other ants. Within 3 hours hundreds of homopterans were carried into the pavilions. In a few cases we also observed that homopterans offered in this way were thrown off the leaf.

Prey and other food sources

Foraging occurred mainly on bamboo, but some *P. arachne* workers were also found on ginger and banana leaves. In contrast, only few individuals were observed foraging on the ground layer of dead leaves, close to their nests.

In spite of many hours of field observations, no act of predation was observed. Dead insects (mosquitoes, grasshoppers, or parts of them) or honey—water—solution were accepted as food. Presentation of larger quantities of food induced recruitment behaviour. *Notobitus affinis* Dallas 1852 and *Cloresmus* species (Heteroptera, Coreidae), bamboo bugs which release honey dew and which are attractive to other ants (MASCHWITZ *et al.*, 1987), were ignored.

Colony foundation

Colony foundation by a single dealate queen took place in a little detritus nest beneath a leaf which resembled a small pavilion (fig. 3).

2.) *Polyrhachis hodgsoni* Forel 1902

Colonies of *P. hodgsoni* sometimes occurred in the same bamboo grove where *P. arachne* lived, but overlapping of the colonies was never observed. The biology of this species was in many aspects similar to that of *P. arachne*.

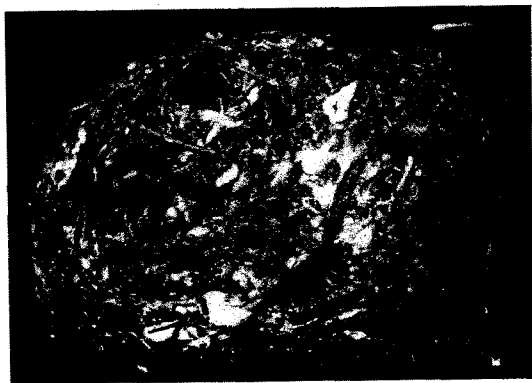


Fig. 3. — Nest of a colony-founding queen of *Polyrhachis arachne*.

Abb. 3. — Koloniegründungsnest von *Polyrhachis arachne*.

In the following, special emphasis is placed on the differences between the two species.

Nest, pavilion, and colony structure

Despite of our intensive search in several colonies, and in contrast to the conditions found in *P. arachne*, no nest was detected in culms of bamboo. In one colony which was collected as a whole a single queen was found inside a large pavilion (24 cm long) together with 196 workers, all stages of brood except pupae, and 60 Pseudococcidae. So this pavilion had to be classified as the nest of the colony. The total number of adults in this colony was 1 queen, 9.192 workers, 81 alate females, and 25 males.

The colony occupied 263 pavilions at two, small bamboo plants (each 1.70 m high, and 4 m crown diameter), about 2 m apart from each other and separated by low grass vegetation. Other colonies lived on much larger bamboo plants (10-15 m high) and their colony sizes may have been larger.

The pavilions were varying in length from 4.5-30.0 cm (median = 17.3 cm, $\bar{\sigma}$ = 17.1 cm, s = 5.3 cm, n = 42) and in width from 1.0-2.5 cm (median = 1.9 cm, $\bar{\sigma}$ = 1.9 cm, s = 0.4 cm). They occupied the whole leaf or only its proximal two thirds. A pavilion normally had 2 entrances, one at its proximal and one at its distal end. A refuse pile was usually present near the latter. The pavilions contained 7-85 workers (median = 34, $\bar{\sigma}$ = 41.6, s = 23.8). During the study time (December to February) females or males occurred only rarely in the pavilions (females : median = 0, $\bar{\sigma}$ = 0.2, s = 0.7 ; median = 0, $\bar{\sigma}$ = 0.1, s = 0.3). Pupae numbered from 0-6 per pavilion (median = 0, $\bar{\sigma}$ = 0.7, s = 1.3), large and medium sized larvae from 0-12 (median = 1, $\bar{\sigma}$ = 3.1, s = 4.1). Small larvae (occurring clustered in large numbers in 8 % of the pavilions) and eggs were not counted.

Weaving behaviour and pavilion building

The most striking difference to *P. arachne* was the mode of pavilion construction : *P. hodgsoni* built its pavilions in longitudinally folded or rolled leaves of broad-leaved bamboo, where the upper side of the leaf formed the interior of the pavilion. Only the small slit between the leaf's edges (normally 1 mm, but up to 1 cm at the ends of the pavilion) was closed with silk and covered with very fine material gnawed off from dry parts of culms and leaves.

In contrast to the conditions in *Oecophylla* species (HÖLDOBLER and WILSON, 1977), the leaves were not actively manipulated. Instead, the ants spun together the edges of a leaf when these happened to move towards each other due to turgor changes resulting from heavy insolation. When a "foraging" worker discovered such a leaf, it immediately recruited nestmates to the site. During several observations, up to 20 workers arrived, up to 5 of

them with larvae which immediately started weaving. This fast and coordinated weaving activity was necessary because the leaves could snapp back rapidly when the sun disappeared again. In addition preformed leaf rolls were used as pavilions, e.g., those produced by climbing plants, spiders, orthopterans, or caterpillars. Weaving behaviour itself was similar to that of *P. arachne* but because of the rolled pavilions the silkwebs were of much smaller size and were woven fine and dense (fig. 4).

Trophobiosis

Homopterans were cultivated in the same manner as in *P. arachne*. *P. hodgsoni* also carried the trophobionts into its pavilions. In the colony which was censused completely aphids were lacking totally but all pavilions contained Pseudococcidae (1-84, median = 41, \bar{x} = 40.8, SD = 27.3, n = 12). In one experiment on Homoptera-acquisition we offered Hormaphididae which had been tended by *Crematogaster* and *Myrmicaria* species on bamboo, and Pseudococcidae from *P. arachne* to a *P. hodgsoni* colony. Within 3 hours most of the hundreds of homopterans were transported into the pavilions (fig. 5).

No statistically significant (Mann-Whitney-U-Test, double sided) differences were found between *P. arachne* and *P. hodgsoni* pavilions concerning numbers of workers, alate females, males, pupae, larvae, Hormaphididae, Pseudococcidae, the sum of homopterans per pavilion, or the sum of homopterans per worker per pavilion. Nevertheless the samples from single colonies showed significant differences between *P. arachne* and *P. hodgsoni*, *P. arachne* always had significantly larger amounts of pupae ($p \leq 0.002$),



Fig. 4. — Pavilion of *Polyrhachis hodgsoni* in construction. Left: pure silk web, right; silk web already with detritus.

Abb. 4. — *Polyrhachis hodgsoni* Pavillon im Bau. Links: reine Seidenfläche, rechts: Seide bereits mit Detritus maskiert.



Fig. 5. — *Polyrhachis hodgsoni* worker transporting a pseudococcid.

Abb. 5. — Arbeiterin von *Polyrhachis hodgsoni* beim Tragen einer Woll-Laus.

homopterans, and homopterans per worker per pavilion (each $p \leq 0.02$) in its pavilions. Also between two *P. arachne* colonies significant differences occurred in numbers of workers ($p \leq 0.05$), and pupae ($p \leq 0.01$). Differences between *P. arachne* and *P. hodgsoni* concerning number of workers, alate sexuals, brood, and trophobionts per pavilion were small and similar to those within the species. Possibly factors like age of colony, availability of food sources, and competition are more important than the differences between the species. No significant differences were found between samples from February 1987 and January 1988, or between colonies inhabiting different species of bamboo.

Other food sources

The foraging behaviour of *P. hodgsoni* is very similar to that of *P. arachne*. On one occasion, *P. hodgsoni* workers were observed coming down a large bamboo and crossing 15 m of bushes to collect electrolytes from several small roots at the margin of a forest stream.

Competitors of *P. arachne* and *P. hodgsoni*

1 out of 11 pavilions (= 9 %) of the completely censused colony of *P. arachne* and 2 out of 20 pavilions (= 10 %) of another colony were occupied

by other ants. In the completely censused *P. hodgsoni* colony this rate was 6 of 269 (= 2.2 %). Table I lists those ants which were found on the bamboos inhabited by *P. arachne* or *P. hodgsoni*.

Table I. — Ants living on bamboo inhabited by *Polyrhachis arachne* or *P. hodgsoni*.

Tabelle I. — Ameisen auf von *Polyrhachis arachne* oder *P. hodgsoni* besiedeltem Bambus.

Ant species	Foraging on bamboo	Occupying <i>Polyrhachis</i> pavilions	Nest at bamboo leaves	Nest in bamboo culms
<i>Tetraponera</i> sp.	X			
<i>Diacamma</i> sp.				X
<i>Leptothorax</i> sp.	X			
<i>Cataulacus</i> sp.	X			
<i>Crematogaster</i> sp.	X 1)			λ
<i>Myrmicaria</i> sp.	X	X 2)		
<i>Pheidole</i> sp.	X	X		
<i>Tetramorium</i> sp.	X	X		
<i>Dolichoderus</i> sp.	X	X		
<i>Tapinoma</i> sp.	X	X 2)		
<i>Technomyrmex</i> sp.	X	X 2)		
<i>Camponotus</i> spp.	X	X 2)		X
<i>Echinopla</i> sp.	X			X
<i>Polyrhachis</i>				
<i>abdominalis</i> Smith 1858	X			X
<i>armata</i> (Le Guill. 1841)	X			X
<i>calypso</i> Forel 1911	X			
<i>inermis</i> Smith 1858	X			
<i>muelleri</i> Forel 1893	X			
<i>plato</i> Forel 1911	X			
<i>rastellata</i> (Latr. 1802)	X	X		
<i>P. (Cyrtomyrma)</i> sp.	X			
<i>P. (Myrma)</i> spp.	X			X
<i>P. (Myrmhopla)</i> sp.	X			
<i>P. (Myrmotherinax)</i> sp.	X	X	X 3)	

1) tending small aphid associations below bamboo leaves

2) with homopterans

3) nest with one queen and four eggs below a leaf of the climber *Mikania cordata* (Asteraceae).

Predators

Calliphorid flies of the genus *Bengalia* were observed stealing larvae from workers of both *P. arachne* and *P. hodgsoni* (fig. 6).

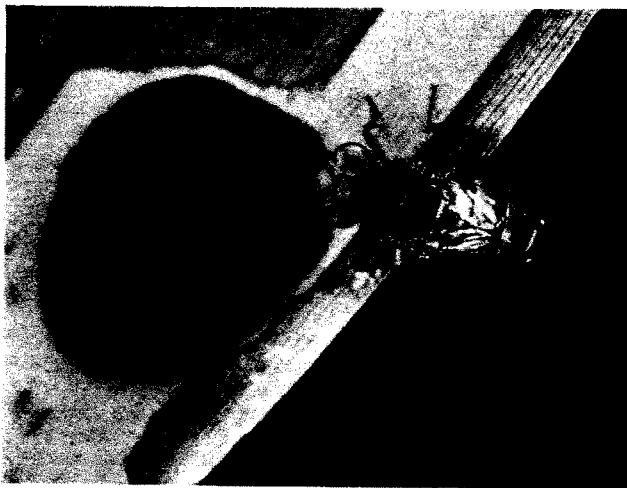


Fig. 6. — Cleptic calliphorid fly of the genus *Bengalia* waiting at the entrance of a nest of *Polyrhachis arachne*.

Abb. 6. — Eine kleptische Calliphoride der Gattung *Bengalia* wartet am Nesteingang von *Polyrhachis arachne*.

2 1/2 days after releasing the Enfluran-treated *P. hodgsoni* colony we observed a cleptic jumping spider at a leaf adjacent to another leaf on which *P. hodgsoni* workers had started to weave a new pavilion with two larvae. With a fast attack the spider stole one larva from a weaving worker and returned to the ant-free leaf to consume it.

Guests

Guests seem to be rare in the nests of the *Polyrhachis* species: Only 2 individuals of a hitherto undetermined species of cockroaches were found in one nest of *P. arachne*. Syrphid larvae were feeding on *Pseudococcidae* in a pavilion of *P. arachne*.

DISCUSSION

Nests and pavilions

The biology of *P. arachne* and *P. hodgsoni* was hitherto mostly unknown. A few authors have described the nests, but in a contradictory manner. BINGHAM (1903) noted that both species are "nesting in the hollow joints of bamboos", while KARAVAEV (1928, 1929) reported *P. arachne* as nesting below bamboo leaves. The only other statement on their nesting habits is from EMERY (1896) who mentioned that nests of *P. arachne* are 6×4 cm large silken chambers below the leaves of palm trees. We suppose that KARAVAEV and EMERY had found pavilions but not nests. The pavilion below a palm tree leaf might be one at the margin of a colony's territory, as was the one we collected below a ginger leaf. All other findings, including those of BINGHAM in Burma, KARAVAEV in Java, and ours in Malaysia, are exclusively from broad-leaved bamboo species.

Different levels of adaptation to an arboreal life are found in *Polyrhachis* (HUNG, 1967). As far as known, all Asian species of the primitive subgenus *Myrma* do not use silk for nest building. They forage both on the ground and on shrubs and trees and nest mainly in the ground, in dead branches on the ground, or in preformed holes in tree trunks (DOROW, unpubl.). The evolution of the use of silk enabled other *Polyrhachis* species to colonize the canopy: Suitable preformed nest cavities were no longer a limiting factor. Instead, nests could be built nearly everywhere in the canopy. The simplest way is to weave nests below or between leaves. This is the most common type of nest in *Polyrhachis* and is used in the subgenera *Cyrtomyrma* (HÖLDOBLER and WILSON, 1983), *Myrmatopa*, *Myrmhopla*, and *Myrmothrinax* (DOROW, unpubl.).

We observed the queen of *P. hodgsoni* in a pavilion, the queen of *P. arachne* in a culm nest. BINGHAM's (1903) finding of *P. hodgsoni* nesting like *P. arachne* (if he was not mixing up pavilions and nests) suggests that there is some flexibility—at least in *P. hodgsoni*, possibly also in *P. arachne*—to switch between the ancient type of nestsite, preformed cavity, and the more evolved type, woven leaf nest. This flexibility enables these ants to maintain their habitat together with their trophobionts even when losing their nestsite to stronger competitors. MUKERJI (1932) states this for the pavilions of *P. lacteipennis* Smith 1858 (*P. simplex* auct.): "occasionally used for temporary housing of the colony". So an accurate delimitation of the categories "nest" and "pavilion" is impossible, since they can be combined. In this connection it is remarkable that brood is not concentrated in the "nest" but is dispersed over the pavilions in *P. arachne* and *P. hodgsoni*. The derived below-leaf type of nest, which reduces the competition pressure for nestsites, is probably given up when the more stable, ancient preformed-cavity type

is available. This seems to be the case in *P. dives* SMITH, 1857, which normally nests freely in large globular nests (YAMAUCHI *et al.*, 1987).

An advantage of the leaf-roll type of pavilion in *P. hodgsoni* might be that this pavilion is difficult to detect for predators and more stable and less material-consuming than the below-leaf type of *P. arachne*. On the other hand, *P. hodgsoni* depends on prerolled leaves for nest and pavilion construction. Our finding that the released *P. hodgsoni* colony built 11 new pavilions within 2 1/2 days suggests, however, that this limiting factor is of low significance for the ants. At present we are unable to assess the value of the leaf-roll-pavilion as a protection against predators: birds quickly learn to specialize on a certain type of prey, and leaf rolls nearly always contain some food for birds (spiders, orthopterans, caterpillars, ants, etc.).

Homoptera cultivation

A remarkable characteristic of *P. arachne* and *P. hodgsoni* is the highly evolved mode of Homoptera cultivation. The ants collect homopterans of different species from all over the bamboo plant and transport them into their silk pavilions. Here they are well protected against weather influences, competing ants, parasites, and predators, a marked advantage for both the homopterans and the ants. The facts that no free-living homopterans were found on the bamboos inhabited by the ants and that some homopterans are thrown down from the leaves suggest that the Homoptera population is regulated by *Polyrhachis* workers according to the ant colony's demands. Such behaviour, which destroys food sources for other ant species, has been reported from *Oecophylla longinoda* (Latreille, 1802) (WAY, 1954), *Camponotus texens* Dumpert 1985 (MASCHWITZ *et al.*, 1985), and occurs also in a pavilion-building *Dolichoderus* species (MASCHWITZ *et al.*, 1989).

Tending of Homoptera in *Polyrhachis* is only known from 3 other species of the subgenera *Cyrtomyrma* and *Myrmhopla*, which are the most evolved subgenera within *Polyrhachis* (HUNG, 1967): *P. (Cyrtomyrma) laevisissima* Smith 1858 (DATTA *et al.*, 1983), *P. (Myrmhopla) dives* Smith 1857 (WASMANN, 1905), and *P. (Myrmhopla) lacteipennis* Smith 1858 (*P. simplex* auct.) (OFER, 1970). According to our extended observations in *Polyrhachis* even the visit of trophobionts is a rare phenomenon. *P. lacteipennis* is able to live in the same habitat as *P. arachne* and *P. hodgsoni*: It has been reported nesting under bamboo sheaths (LEFROY and HOWLETT, 1909), but is not specialized on these plants (HINGSTON, 1929; KARAVAIEV, 1928; LEFROY and HOWLETT, 1909; OFER, 1970).

Similar cases of cultivation of Homoptera in other pavilion building tree ants have been reported from *Oecophylla longinoda* (WAY, 1954), some silk weaving *Camponotus* (Karavaievia) species (MASCHWITZ *et al.*, 1985; DUMPERT *et al.*, 1989), and a silk weaving species of *Dolichoderus* (MASCHWITZ *et al.*, 1989). But all these species show no plant specialization.

Plant specialization

Normally only ants living in mutualistic symbiosis with plants are specialized on distinct host plant taxa. In such systems, both ants and plants have developed coadaptations for their mutual benefit. In the *P. arachne*- and *P. hodgsoni*-bamboo association no specific adaptations were found in the plants. The ants, on the other hand, are apparently able to detect and select different species of broad-leaved bamboo as their habitat. The advantage of this specialization for the ants seems to be as follows: *P. arachne* and *P. hodgsoni* have large colonies. If such a colony gains its food mainly from Homoptera, collected in a large area and gathered in some pavilions, it is necessary to provide the mono- or at least oligophagous aphids and pseudococcids with their proper food plant. While in a tropical rainforest plants of the same species are only rarely clustered at one site but normally are scattered over a large area, the abundant and monophytous bamboo thickets warrant the proper food for the Homoptera in an optimal way. It is unclear up to know whether the ants should be regarded as parasites of bamboo because of the phloem sap loss caused by their homopterans, or are even beneficial for the plants by protecting them against phytophagous animals and by controlling the number of homopterans.

Competitors

On the studied bamboo plants occurred a large number of other ants, competing for (a) nest space in bamboo culms, (b) foraging area, and (c) trophobionts (table I).

P. arachne and *P. hodgsoni* were never found nesting in bamboo culms lying on the ground, possibly due to strong competition from other ants nesting or foraging there. These are favored nestsites of other aggressive ant species with large colonies, e.g., of the genera *Camponotus*, *Leptogenys*, and *Odontomachus*. In addition, culms on the ground decay faster and cannot serve as a long-term nestsite.

The ecological specialization of *P. arachne* and *P. hodgsoni* leaves many niches for other species of ants on the same bamboo plant: Small species like *Crematogaster* can nest in bamboo culms too small for *P. arachne* and *P. hodgsoni* and can exploit food sources effectively by fast recruitment combined with effective fighting ability. They do not control a larger area but defend their trails and the surroundings of a food source (personal observations).

P. arachne and *P. hodgsoni* are only active during daytime. This leaves niches for ants active during the night. One species of *Polyrhachis* (*Myrma*) with a small colony size was found twice, one time nesting in an internode between two internodes occupied by *P. arachne*, the other time in an internode adjacent to a *P. arachne* nest. This species of *Polyrhachis* (*Myrma*) was not active during daytime. Also a nest of a colony founding queen of *Poly-*

rhachis (*Myrmotherinx*) was tolerated by *P. hodgsoni* at its host plant. This is surprising, for many ants are known to kill systematically colony founding queens within their foraging area (HÖLDOBLER and LUMSDEN, 1980). Further observations are needed to evaluate, which special adaptations make these unusual kinds of coexistence possible.

Possibly due to the relatively large colony size of the two *Polyrhachis* species their pavilions are only rarely taken over by other ants. Such takeovers happen only at the margins of the colonies' territories.

P. arachne and *P. hodgsoni* show a new kind of territorial strategy, combining aspects of the absolute-territory strategy of *Oecophylla longinoda* with the spatiotemporal strategy of other species (terminology of HÖLDOBLER and LUMSDEN, 1980): Like *Oecophylla* the two *Polyrhachis* species effectively decentralize their home bases, which enables them to control a large area. But unlike *Oecophylla*, *P. arachne* and *P. hodgsoni* use a spatiotemporal-territory strategy, only defending the close vicinity of their pavilions and food sources.

The two ant species have very similar life habits, which should result in intense competition. Surprisingly, we found no evidence supporting this prediction. The reason, at the moment, remains open.

Predators

Calliphorid flies of the genus *Bengalia* were observed stealing larvae of *P. arachne* as well as those of *P. hodgsoni*. These flies are known to be cleptic at some ant species (MASCHWITZ and SCHÖNEGGE, 1980) but are here reported for the first time for *Polyrhachis*. Cleptic spiders stealing ant brood are mentioned in the literature only twice: An undetermined spider stole larvae of *Megaponera foetens* (Fabricius, 1793) in former Rhodesia (ARNOLD, 1914), and *Menemerus bivittatus* (Dufour, 1831) (*Marpissa melanognathus* auct.) (Salticidae) stole brood of *Solenopsis geminata* (Fabricius, 1804) in India (BHATTACHARYA, 1936). The specialization on stealing ant brood seems to be quite common in the tropics and was observed by the senior author with different species of Salticidae and Formicidae being involved. This seems to be due to the fact that in the tropics weaver ants frequently have to carry their larvae to different nests or pavilions. In addition, the nest sites of many ant species are changed very often due to a bivouac mode of life or strong competition, all resulting in a frequent transport of brood.

ACKNOWLEDGEMENTS. — We thank Prof. YONG HOI SEN and Prof. KIEW BONG HEANG (University of Malaya, Kuala Lumpur), Dr. THO YOW PONG, WULF KILLMANN and his gtz-research team (Forest Research Institute, Kepong, Malaysia) for their kind help during all our studies in Malaysia, including the providing of laboratory and field station facilities. Dr. Claude BESUCHET (Museum d'Histoire Naturelle, Geneva), B. BOLTON (British Museum (Natural History, London), Dr. Michael BRANCUCCI (Natural History Museum, Basel), Dr. Janine CASEVITZ-WEBBERSSE (Museum National d'Histoire Naturelle, Paris), Dr. Rudolf KOHOUT (Queensland Museum, Brisbane), Dr. Valter RAINERI (Museo Civico Di Storia Naturale,

Genova), and Prof. Edward O. Wilson (Museum of Comparative Zoology at Harvard University, Cambridge U.S.A.) have kindly loaned specimens of *Polyrhachis*. We thank JEANNETTE and George C. WHEELER (Silver Springs) for their informations about enemies of ants and KONRAD FIEDLER and RÜDIGER KLEIN (University of Frankfurt) for helpful comments on the manuscript. Field work was supported by the Deutsche Forschungsgemeinschaft.

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