

## The migrating herdsman *Dolichoderus (Diabolus) cuspidatus*: an ant with a novel mode of life

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**Summary.** The Malayan ant *Dolichoderus cuspidatus* lives in obligatory symbiosis with the pseudococcid *Malaicoccus formicarii* and other species of the same genus. The assemblies, which may be encountered up to 25 m away from the nest, are constantly covered with a great number of worker ants who protect them and receive honeydew. In the event of heavy rain the workers form a dense protective cluster, clinging to each other on top of the mealybugs. Neither hunting behavior nor active search for protein sources was observed in *D. cuspidatus*, although dead insects were accepted as food. When not searching for new plants, the activity of the ants outside the colony is limited to visiting the mealybugs. During the night and parts of the day the ants stay in their nest. Ant colonies deprived of their mealybugs are not viable due to their dependence on the symbiosis and because of the competition of other ants. Antless *M. formicarii* are likewise not viable. The mealybugs are extremely polyphagous and feed on many different monocotylous and dicotylous angiosperms. They feed exclusively on the phloem sap of young plant parts which are rich in amino acids. *Dolichoderus cuspidatus* workers carry the mealybugs to such locations. During the picking up and carrying process both partners display typical behavioral patterns. The colonization of new feeding sites takes place in well organized mass processions. During the foundation or disintegration of large feeding complexes, provisional depots with waiting mealybugs and ants are set up. The pseudococcids are carried not only while shifting the feeding sites, but also whenever the colony leaves its former nesting site and especially when any kind of disturbance occurs. They are even carried about without any apparent external cause, which leads to the fact that, at all times of trail activity, on average more than 10% of all ants using the trails carry mealybugs. Mealybugs are also present within the nest, especially adult females which are vivi-

parous and give birth to their offspring there. Censused colonies each consisted of over 10000 workers, about 4000 larvae and pupae, more than 5000 mealybugs and one ergatoid queen. Male winged ants were observed in large numbers during the dry season (January–February) and during the rainy season (September–October). The colonies form typical clumplike bivouac nests consisting of clusters of workers clinging to each other, thereby covering the brood and the mealybugs. The nesting site is in no way altered by constructive measures and is mostly found close to the ground. The preferred nesting sites are clusters of leaves, and cavities in wood or soil, although a freely hanging bivouac between a few branches may be set up as well. As soon as the distance between the nest and the feeding site is too great the colony moves to the feeding site, whereby the brood and the mealybugs are carried along in a well organized manner. During such nest-moving the establishment of intermediate depots can be observed. A shift of nest sites can also be induced by disturbances or by a change in the microclimate in the vicinity of the nest. Colonies multiply by budding. The tropical rain forest continuously offers different sprouting plants, the utilization of which requires extreme mobility on the part of the consumer. The unique behavioral strategy of *D. cuspidatus*, to carry constantly their polyphagous mealybug partners to new feeding sites and to take the whole colony there has enabled this ant and its symbiont to occupy this rich food niche. *Dolichoderus cuspidatus* is the first true nomad found in ants.

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### Introduction

Nomads are stock farmers who subsist from their livestock and who closely coordinate their life style with that of their livestock, for instance, by follow-

ing them to the pastures these need. Several ants with a predatory mode of life, especially the various army ants of the new and old world tropics, who frequently change their nesting site and thus enter new hunting areas, have been called nomadic. However, these migrating hunters are not true nomads in the genuine sense of the word.

During earlier research in the rain forests of the Malayan peninsula we encountered an ant with very conspicuous behavior. On fresh shoots workers of *Dolichoderus cuspidatus* formed dense clusters which covered assemblies of small, agile, brownish, aphid-like homopterans, the pseudococcid *Malaicoccus sp.*, mostly *M. formicarii*. When disturbed the ants gripped their mealybugs with their mandibles and carried them away. An extensive trail system led to a nest in which the ants were found, almost without cover, in a dense cluster of workers, brood, and mealybugs above the ground amidst the vegetation. It was observed that while nest-moving not only the brood but also the mealybugs were taken along. The question arose whether this could be a true case of a migrating herdsman, a nomad, whose life history is highly adapted to that of its trophobiotic partner. A species with such a mode of life has so far not been discovered in ants or other animals. With the above-mentioned questions in mind we analyzed the sociobiology of this species more closely, giving special attention to the trophobiotic relationship to the mealybugs. Nesting and migratory behavior were investigated as well as colony multiplication. The biology of the symbiosis partner was covered as far as necessary.

## Methods

The investigations were mostly carried out from September 1982 to February 1983 in West Malaysia, mainly at the Gombak Field Centre of the University of Malaya in the Gombak Valley. The station is situated in the western coastal mountains near Kuala Lumpur which are covered by rain forest. Dry seasons are not very marked in this region. Details of the methods are explained in the text.

## Results

### *The distribution of the symbiotic assemblies between Dolichoderus cuspidatus and Malaicoccus sp.*

The first step in answering the question whether *D. cuspidatus* and *Malaicoccus* live in a close or even an obligatory symbiosis was to locate and inspect as many ant colonies as possible. The results are depicted in Table 1. The ant is distributed over vast areas of the Malayan peninsula where it was found in primary forests and at its edges and in not heavily disturbed secondary forests. In all 52 recorded colonies *D. cuspidatus* was found to be associated mostly with *Malaicoccus formicarii*, but also with *M. takahashii*, *M. moundi*, *M. khooi* and a further *Malaicoccus* species not yet described (Williams, personal communication). In eight cases minor additional associations with aphids (on *Vitex pubescens*), other coccids (on *Zingiber spectabile*) and with membracids (on *Piper aduncum*) were observed. These partners were treated in a different manner to *Malaicoccus*. Despite long periods of observation at different times of the day while simultaneously disturbing the ants (10 observations over 10 min each with

**Table 1.** Localities where *Dolichoderus cuspidatus* has been found. All colonies were associated with *Malaicoccus*, some additionally with other homopterans. At the collection localities of *Malaicoccus* known from literature at Kuala Lumpur, Kepong and Ulu Langat (Selangor), Frazer's Hill, Cameron Highlands and Riouw Islands (Indonesia, near Singapore) the ants were not identified to species level (Williams 1978)

Collection locality	Location	Number of nests	Species of <i>Malaicoccus</i>	Number of additionally observed homopteran associations
Ulu Gombak (near Kuala Lumpur)	At the edge and in the interior of primary and secondary forest	28	<i>M. formicarii</i>	8 (with membracids, coccids and aphids)
Genting Highlands (near Ulu Gombak)	At the edge of secondary forest	12	<i>M. moundi</i> , <i>M. khooi</i>	0
Maxwell Hills (north-west coast, ~1000 m altitude)	In primary forest	4	<i>M. sp.</i>	0
Bukit Bauk (east coast, lowland)	At the edge of primary forest	1	<i>M. formicarii</i>	0
Mentekap (central peninsula, lowland)	At the edge of secondary forest	3	<i>M. formicarii</i>	0
Pasoh (southern central peninsula near Seremban, lowland)	In primary forest	2	<i>M. takashii</i>	0

**Table 2.** Angiosperms, on which *Dolichoderus cuspidatus*/*Malaicoccus* sp. associations were found. (Further feeding plants of *Malaicoccus*, which are known from literature, are *Rubus*: Rosaceae; *Alpinia* = *Languas*: Zingiberaceae; bamboo: Poaceae; *Poikilospermum cordifolium*: Urticaceae; *Palaquium obovatum*: Sapotaceae; see Williams 1978). t = tree; h = herbaceous plant; s = shrub; c = creeper; f = fresh shoots; l = young leaf; fl = flowers; fr = young fruits

Order	Family	Genus and species	Type of plant				Sucking site			
			t	h	s	c	f	l	fl	fr
Liliatae	Araceae	<i>Colocasia</i> (2 species)		×					×	
	Liliaceae	<i>Smilax</i> sp.				×	×			
	Zingiberaceae	<i>Zingiber spectabile</i>			×		×	×		
Magnoliatae	Piperaceae	<i>Piper aduncum</i>	×				×	×		
	Melastomaceae	<i>Melastoma malabaricum</i>			×		×			×
	Hypericaceae	<i>Mesua kuenstleri</i>	×				×			
	Caesalpiniaceae	<i>Saraca declinata</i>	×				×			
	Caesalpiniaceae	<i>Bauhinia</i> sp. <sup>a</sup>				×	×			
	Mimosaceae	<i>Mimosa</i> sp.				×	×			
	Fabaceae	<i>Millettia atropurpurea</i>	×				×			
	Aceraceae	<i>Acer caesium</i>	×				×			
	Euphorbiaceae	<i>Macaranga</i> sp.	×				×			
	Euphorbiaceae	<i>Glochidium</i> sp.	×				×			
	Lecythidaceae	<i>Barringtonia</i> sp.	×				×			
	Anonaceae	<i>Polyathia</i> sp.	×				×			
	Anonaceae	<i>Goniothalamus macrophyllum</i>	×				×			
	Tiliaceae	<i>Grevia tomentosa</i>	×				×			
	Moraceae	<i>Ficus</i> sp.	×				×			
	Moraceae	<i>Artocarpus elasticus</i>	×				×			
	Moraceae	<i>Uncaria</i> sp. <sup>a</sup>				×	×			
Solanaceae	<i>Solanum indicum</i>			×		×				
Verbenaceae	<i>Vitex pubescens</i>	×						×	×	
Asteraceae	<i>Mikania cordata</i>				×	×				
Asteraceae	<i>Eupatorium odoratum</i>			×		×				

<sup>a</sup> Known also from literature

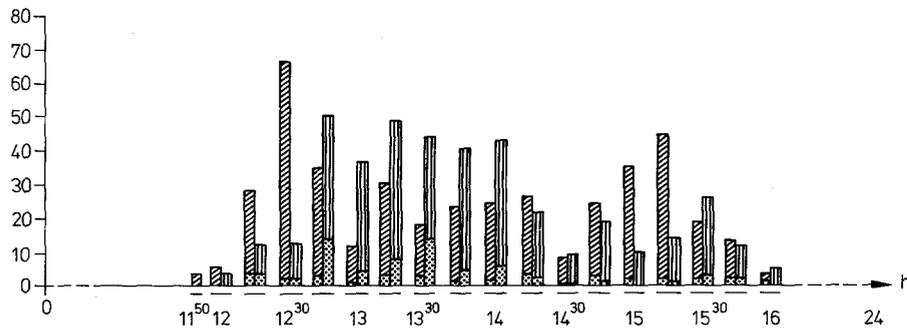
aphids, 5 observations over 10 min each with membracids and coccids) the typical carrying observed with *Malaicoccus* could never be induced. While the aphid and membracid groups were separated from the "ant-own" mealybug associations, one of the two observed coccid associations lived among a *M. formicarii* – *D. cuspidatus* association. When this association was disturbed, only *M. formicarii* was unerringly grasped and carried away. We also tested whether the *Malaicoccus* species mentioned above are associated with other ant species. We undertook a quantitative survey along a 3 km stretch of road in our main investigation area Ulu Gombak where *D. cuspidatus* was frequently found associated with *M. formicarii*. All accessible plants (approximately 1000), which we knew to be food plants of *Malaicoccus*, were thoroughly scrutinized for trophobiotic associations with other ants. We found 50 different trophobiotic associations with 18 different ant species of various subfamilies (*Pheidole* spp., *Cremastogaster* spp., *Myrmecaria* spp., *Oecophylla smaragdina*, *Anoplolepis longipes*, *Camponotus* spp., *Technomyrmex* spp., *Dolichoderus* spp.). Among these were further *Dolichoderus* species which were associated with coccids, aphids and membracids. In no case were *Malaicoc-*

*cus* species found. In addition, *Malaicoccus* species were not normally found to be symbiosis partners of other ants, although more than 1000 homopter-an-ant associations were inspected in the course of 5 months all over Malaysia. One exception was found, however: *M. khooi* was partly associated with *D. (Hypoclinea) tuberifer*, which has a similar life style to that of *D. cuspidatus* (unpublished data).

### Food plants

The exploitation of the food resources accessible to phytophagous animals mainly depends on the degree of their polyphagy. We examined which plants belong to the diet of *Malaicoccus*. Table 2 reflects broad polyphagy. This confirms existing records (summarized in Williams 1978). The mealybugs suck on plants from both classes of angiosperms: among the Magnoliatae on representatives of 5 of the 6 subclasses (Magnoliidae, Rosidae, Dilleniidae, Asteridae, Hammamelidae) in 13 out of 61 orders, and among the Liliatae on representatives of 2 of the 3 subclasses (Liliidae, Arecidae) in 3 out of 17 orders (system after Ehrendorfer 1983). Table 2 also shows on which parts of the

Animals/min



**Fig. 1.** Trail activity of a typical *Dolichoderus cuspidatus* colony during 24 hours (rainy season).  
 ▨ Workers leaving the nest;  
 ■ Workers returning to the nest;  
 ▩ Number of workers carrying mealybugs

plants the mealybugs suck. They feed exclusively on the phloem sap of young, growing plant parts such as young shoots and leaves, unfolding blossoms and young fruit.

#### Feeding sites and trail system

The feeding sites were occupied by mealybugs in numbers of 20 up to several hundred, which were visited by numerous workers, e.g. in three single countings 75, 105, 273 mealybugs were visited by 60, 65, 148 ants respectively. The mealybugs were nearly completely covered by workers. Seven examined colonies had 4–18 feeding sites on small trees, shrubs, and herbs. They were located at distances from 2 to more than 20 m from the nest. Four colonies had one main trail, two colonies had two and one colony three different trail systems which led in different directions. The main trails divided into several subtrails which led to the various feeding sites. The actual distance run by the ants was much farther than the beeline distance, because they never gave up the old trails on which they had found the feeding sites. These were often very complicated routes over climbers and other vegetation. In one instance we found a colony 2 m from the feeding site after having painstakingly followed the trails in the trees for 25 m.

The mealybugs are not only transported when the feeding sites are disturbed but also under normal conditions. Figure 1 shows how many ants moved on the trails and how many of them carried mealybugs at 15 min intervals. From that and from further activity measurements, we can conclude some remarkable facts. First, there is no traffic at all during the night. Moreover, the ants do not frequent the trails at all times of the day. Even at the times of inactivity ants still cover and protect the mealybugs at the feeding sites. Activity started in the rainy season between 1100 and 1200 hours but in the dry season between 0800 and 0900 hours. During the activity period mealybugs of all ages

were permanently carried to and from feeding sites. On average, of all the ants running on the trails 11% carried mealybugs.

#### Shifting of feeding sites

As mentioned earlier, the mealybugs feed exclusively on freshly growing parts of the plants. This means that especially young leaves or flowers can be fed upon only for a short time. In colonies with freshly colonized feeding sites, we never found ants outside the established trail system. Presumably the search for new sites is a distinct process performed by many ants. In several cases we could observe the natural process of colonization. In one instance a main feeding tree broke in two and the ants had to look for new sites. In one day they removed all the mealybugs from the tree and brought them to the nest. Half a day later a completely new trail system branched off from the original route to end up in new trees and twigs. All the sites on leaves and branches which were too old were abandoned by the ants some hours later. On the third day they had all found new feeding sites for their mealybugs. Two days later the whole area was deserted by the colony. Feeding site colonization could be triggered experimentally by cutting off all food plants of one colony and putting them down close to the nest. The ants carried their partners to an intermediate depot within 3 h and brought them back to the colony later. After a further 2.5 h there was a new intermediate mealybug assembly in the vicinity of the nest. Within 24 h they colonized new feeding sites from this point. These were partly deserted after 24 h and more new sites were colonized. The formation of intermediate depots could be observed during the normal colonization process as well.

How are new feeding sites discovered? The following excerpt from our records provides an explanation:

(A) 0735 hours: 8 workers appear at a distance

of 1 m from a strongly frequented trail on the stem of a small *Piper* tree. 0800 hours: 4 ants without mealybugs examine the tip of the branches intensively. 0855 hours: 8 ants on a shoot tip, 1 mealybug is put down. 0910 hours: 13 workers on the shoot, several small mealybugs are sucking calmly. Ants leaving the feeding site lower their gaster in a typical way indicating that they are recruiting nest mates by trail laying. 0945 hours: more than 30 workers and 20 mealybugs are present, a small feeding site is established.

(B) 1030 hours: On an older *Piper* leaf 4 ants put down 3 mealybugs. Because they are crawling around without sucking they are picked up again within half an hour and disappear with the ants. Obviously the mealybugs did not accept this part of the plant.

#### *Non-trophobiotic nutrition*

Under natural circumstances we did not observe *Dolichoderus cuspidatus* obtain carbohydrates from sources other than trophobiotic partners. When we offered concentrated honey solution near a trail, single ants fed on it but there was no food alarm. Continuous observation of *D. cuspidatus* over several days at trails near the nest showed that thousands of mealybugs were transported whereas not a single dead arthropod was carried into the colony. Occasionally ants were seen carrying home faeces particles, presumably of birds or reptiles. The scarcity or the lack of insect transports under natural conditions indicates that these ants neither hunt nor actively scavenge for dead insects. Because this is an important question for the understanding of the symbiosis relationship, we investigated the reaction of ants towards offered protein food. When we offered dead insects near the trails or close to the nest and single ants were cautiously placed near the objects, within a few minutes these workers brought other ants to this place. On their way back to the colony they apparently laid an alarm trail by pressing the gaster to the ground. The newly arriving ants gripped transportable parts of the insects and dragged them to the nest. They fed on the bigger parts for some time but had great difficulties dismembering the larger parts. Carrying such parts to the nest took them longer than an hour, because there was no cooperation during the transportation process even when the objects were densely covered with conspecifics. As shown later, the ants can overpower living arthropods which chance upon a feeding site; such intruders are dissected and transported to the nest.

Thus in principle they are able to catch arthro-

pods. How then, can the fact be explained that we never observed ants carrying prey to the nest under natural conditions? To clarify that question we investigated the behavior of the ants in the nest periphery where formicids usually hunt and compared it with the behavior of other tree-living ants in the same area which feed on honeydew as well. We chose four different sites which consisted of 140 leaves of various plants (surface approx. 0.4 m<sup>2</sup>) which were located close to the *D. cuspidatus* feeding sites or to the main trails. We observed for 10 min at each site, but although there were numerous ants close by, not a single *D. cuspidatus* worker investigated a leaf systematically in the 40 min. Only two ants ran a short distance across one of the leaves within the observation site. During this time 56 ants from 5 genera (in the sequence of frequency: *Technomyrmex* sp., *Polyrhachis* sp., *Myrmecaria* sp., *Camponotus* sp., *Diacamma* sp.) visited the observation area. They searched every leaf intensively as is typical for ants hunting on trees. Thus *D. cuspidatus* never hunts or searches for dead animals within its territory, but exclusively visits its mealybugs. We could not substantiate whether *D. cuspidatus* devours surplus trophobiotic partners to obtain animal protein as reported from *Lasius flavus* (Pontin 1958, 1961, 1978). In litter collected under freely hanging nests we never found any remnants of dead larvae or exuviae. Possibly the waste is transported further away or dead mealybugs are sucked out at the feeding sites. Mealybugs which were killed and squashed were licked at and carried around. It is remarkable that the ants readily feed on mammal urine and also recruit new workers to it.

#### *The behavior of the symbiosis partners at the feeding sites*

*Behavior of the mealybugs.* In 1954 Reyne reported that *Hippeococcus*, which is closely related to *Malaicoccus*, does not produce honeydew. This is not true for *Malaicoccus*. When we observed the mealybugs at the feeding sites, which was rather difficult because of the permanent layer of ants covering the pseudococcids, we noticed small drops of liquid oozing out of the anus of the mealybugs. There they adhered to the numerous long bristles (trophobiotic organ) on the body and were immediately consumed by one of the ants (Fig. 2). When tested with a sugar reagent (Dextrostix, Merck) large amounts of sugar obviously originating from the plant phloem were detected. The honeydew was always excreted spontaneously. Its release was not induced by antennal drumming as



**Fig. 2.** Sap-sucking *Malaicoccus formicarii* larvae separated from *Dolichoderus cuspidatus* have assembled after wandering about for hours. As their honeydew has not been removed by their ants, it has gathered in large droplets at their long-haired body end (trophobiotic organ)

in many homopterans visited by ants. The drops were different in size. In 3 observed 2<sup>nd</sup> instar larvae we recorded the following intervals between the excretions: (1100 hours, sunshine) 15–20 s: twice; 21–30 s: 8 times; 31–40 s: once; 41–50 s: 8 times; 51–60 s: 3 times; 61–70 s: once. Other mealybugs of this association did not excrete at all in the 2 min of observation; this was probably because they were not sucking at that time.

When disturbed, not only the ants but also the mealybugs began to move excitedly. Single mealybugs crawled on top of ants but were removed quickly with the mandibles. While small mealybugs were merely picked up, often several at a same time, the disturbed big mealybugs raised their bodies thus inviting the ants to pick them up. The seized mealybugs remained motionless while being carried. Even when the ants were removed cautiously from the feeding site the mealybugs dis-

played signs of disturbance and began to move about restlessly. Obviously the absence of the ants was quickly noticed.

*The behavior of the ants.* As mentioned before, the ants cover their mealybugs continuously, forming dense layers on them. They incessantly touch their “livestock” with their antennae and move about to collect honeydew. The protection of the mealybugs was conspicuous during heavy rain falls. On such occasions the ants formed large clusters resembling tents over their pseudococcids by clinging to each other (Fig. 3).

Even a slight mechanical disturbance caused the mealybugs to be picked up. Adult females and big larvae are taken first. This phenomenon was noticed by the first observers of these mealybugs (Takahashi 1950, 1951; Williams 1978). But even without the external mechanical stimuli single mealybugs were carried away from the feeding sites. When disturbed, the ants gripped the big larvae and adult females by the head whereupon they let go of the plant (Fig. 4). During transport the mealybugs remained motionless, except for a certain play of their antennae on the head of the ants. Small and medium larvae were picked up by any part of their bodies while the ants made nodding movements with their heads in the direction of the mealybugs. Up to five larvae were carried simultaneously mostly as a small bunch of mealybugs clinging to each other (Fig. 5). Between a few minutes and half an hour after the disturbance the mealybugs were either replaced or carried away.

The ants reacted very aggressively towards other arthropods at their feeding sites. To test this, different animals such as spiders, crickets, and beetles 5–12 mm in length were held into the worker clusters for 1 s. In 6 out of 15 cases these arthro-



**Fig. 3.** Shelter of clustered workers of *Dolichoderus cuspidatus* on *Piper aduncum* protecting their mealybugs against heavy rain



Fig. 4. *Dolichoderus cuspidatus* worker carrying a female imago of *Malaicoccus formicarii*



Fig. 5. *Dolichoderus cuspidatus* worker carrying several larvae of *Malaicoccus formicarii* clinging to each other

Pods were immediately attacked and seized with the mandibles, so that they could not free themselves. They were killed and carried away within 1 h. This aggressiveness offers an explanation for the fact that no predators or parasites were ever observed at the feeding sites. Even the nest did not contain any parasites or guests. When we placed unguarded mealybugs near a trail, the ant which found them recruited nestmates to carry them away. This was never the case with membracid, aphid or other coccid species.

#### *Nest site and nest structure*

The search for the hidden and sometimes lofty nest sites was difficult and time-consuming because of the nearly impenetrable vegetation, the limited daily activity of the ants, and their susceptibility towards disturbance. Therefore we were unable to localize the nests of all feeding associations discovered. Table 3 shows the extreme flexibility of the ants when selecting their nest sites. In the sec-

Table 3. Location and exposition of 64 nesting sites of *Dolichoderus cuspidatus*

Location of nesting sites		Exposition of nesting sites	
Subterranean	5 (8%)	Largely secluded in ground or tree cavities	15 (23%)
Directly on the ground	4 (6%)	In dense vegetation	46 (72%)
In the herbaceous and shrub zone below 2 m high (also in bamboo stems)	50 (78%)	Mostly exposed	3 (5%)
On trees	5 (8%)		

ondary forest of the Gombak Valley we found them mostly close to the ground. However, they were also found directly on the ground, under the ground, and in trees. Most colonies were within dense living or dead vegetation. Sometimes they nested in nearly closed cavities or hung almost completely free in shady vegetation.

Most colonies formed more or less concentrically clumped gatherings of ants in the vegetation (Fig. 6). When necessary, however, they were able to adapt to special local nesting sites, e.g., internodes of fallen bamboo stems where the ants settled quite often (Fig. 7) or a long gap between two living tree trunks. As in all other cases no trace of nesting material was found in the cavity.

The animals of this nest and of one other colony were counted when the ants were not active (Table 4). They both contained more than 10000 worker ants and over 4000 larvae and pupae. In one case 7% of the ants were outside the nest at the feeding sites, in the other colony 51% were found outside. Both colonies and two other nests contained only one wingless ergatoid queen which instead of the conspicuous spines on the pro- and metathorax of the workers has only big lumpy elevations. The length of the gaster (3.5–4 mm) is significantly larger than that of the workers (2.2 mm). Both colonies possessed a large number of mealybugs (3600 and 5200), 43% and 32% of which were found within the nest. Strikingly, 90 and 95% of the adult female mealybugs were located in the colony. When isolated, they could be observed reproducing viviparously. Male mealybugs were never found.

We did not find male ants in all colonies, nor in certain seasons. In some of the nests we found males during both the dry and the rainy seasons of 1973 and 1982. They appeared on the surface of the colonies in the afternoon.



Fig. 6. Colony of *Dolichoderus cuspidatus* hanging freely in a bush

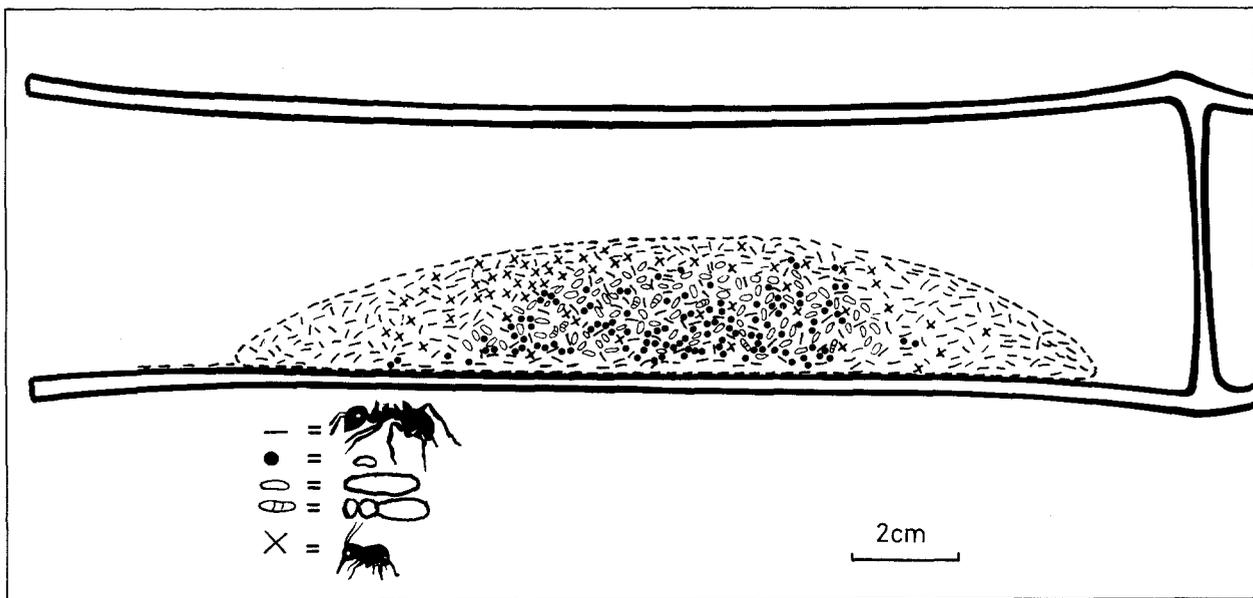
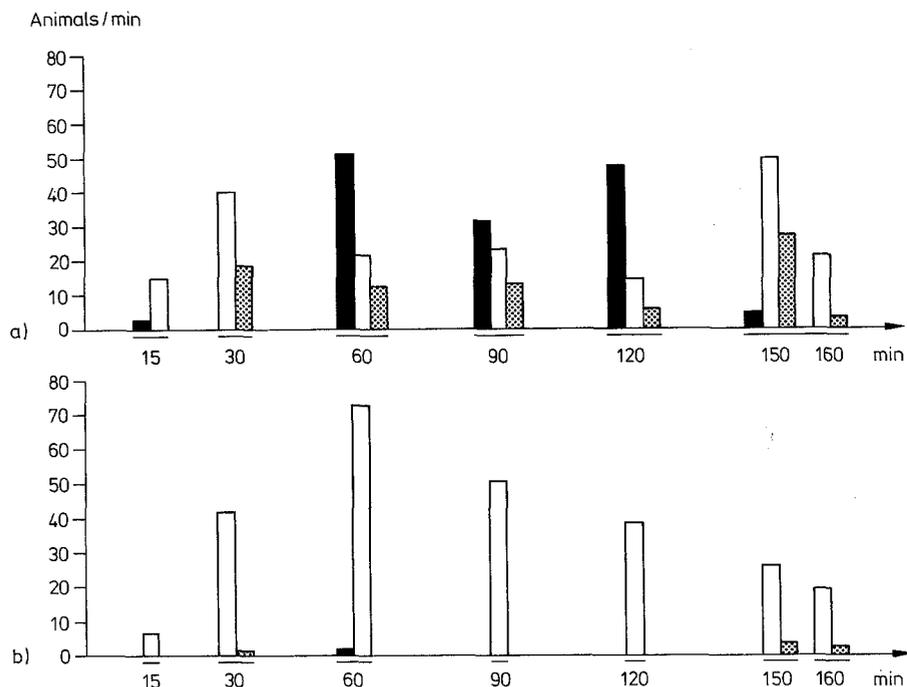


Fig. 7. Structure of a bivouac nest within a dead horizontally lying bamboo stem. The animals were quickly killed with liquid chloroform

Table 4. Colony size and colony composition of two colonies of *Dolichoderus cuspidatus*. Nest 1 was collected before the beginning of their day-time running activity (0800 hours), nest 2 after the termination of their running activity (1900 hours). The number of eggs present were not counted in either nest

Number of nest	Mealybugs in the nest		Mealybugs at the feeding sites		Total number of mealybugs	Queens	Workers in the nest	Workers at the feeding-sites	Total number of workers	Larvae			Larvae total	Pupae
	Adults	Larvae	Adults	Larvae						Small	Medium	Large		
Nest 1	704	850	31	2059	3644	1	12752	950	13702	323	429	575	1327	3038
Nest 2	315	1379	222	3313	5229	1	5344	5537	10881	-	-	-	3053	1010



**Fig. 8a, b.** Temporal course of nest-moving in *Dolichoderus cuspidatus*. Number of workers leaving the old nest **a** and returning to it **b**. □ Workers not carrying objects; ▨ Workers carrying mealybugs; ■ Workers carrying brood

### Nest-moving behavior

The absence of any building activity, the wide spectrum of nesting sites, and the permanent changing of their food plants indicate that *D. cuspidatus* moves quite often. Even slight changes of the nest surroundings such as the removal of some shading leaves caused a nest change.

A change of nesting site is graphically depicted in Fig. 8. During a nest change the ants transported brood and mealybugs. Obstructions in the route such as small gaps between branches were overcome by forming bridges of workers as in army ants. During nest-moving no mealybugs were transported to the feeding sites. At its termination transport commenced again. The whole change of a nest over a short distance lasted between 2 and 3 h. In such cases no formation of intermediate assemblies was observed, in contrast to long-distance movement (15–25 m) where intermediate depots were formed. Hereby ants and mealybugs gathered on leaves or branches for several hours. The mealybugs and the ants at the feeding sites did not show any sign of excitement during nest-moving, an indication that this is an everyday affair. Although we observed nest-shifting under natural conditions quite often (Table 5), we could not find any periodicity in nest-moving. The frequency varied from one or two nest-movings per week up to none in 15 weeks.

The distance moved varied between 0.5 and more than 25 m. According to our observations

**Table 5.** Nest-moving frequency of 12 colonies of *Dolichoderus cuspidatus*

Observation time in weeks	Number of nest-movings
1/2	1
1	1
3	3
3	1
4	5
8	6
8	2
10	6
11	9
11	2
12	1
15	0

there is a correlation between nest-moving and changing of feeding sites. When the distance became too great, the whole colony followed although mostly after a delay of several days. When the new nest sites were located far away in almost inaccessible vegetation, the colonies were occasionally lost from sight.

### Colony multiplication and passing on of the symbiotic mealybugs

All the results mentioned so far prove the extremely close relationship between these ants and their mealybugs. One basic precondition for the development of such a close symbiosis is the passing

on of the pseudococcids from one nest generation to the next. In principle to achieve this, the pseudococcids must either be taken along by the queen during mating and the colony foundation process or the symbionts must be passed on during the budding of the colony. The pattern of the colony distribution indicated the latter. The Gombak road sides were precisely checked for symbiotic assemblies. At five places, 2–4 colonies at a distance of 10–30 m were found, whereas for hundreds of meters or even for miles no further colony could be found although the sites seemed suitable. In one case we could observe the budding of a colony directly: a group of ants built up a new trail system and colonized a new feeding site (November 1, 1982). Eight days later we discovered that one part of the colony had moved to these new grounds and founded a filial nest, while the other part of the colony had moved close to the old feeding site.

#### *The interdependence of the symbiosis partners*

All results obtained so far indicate that the symbiosis of *D. cuspidatus* with *Malaicoccus* is an obligatory partnership in which the partners depend on each other. To clarify whether the partners are viable singly we undertook isolation experiments.

*Ants without mealybugs.* A complete colony including its feeding associations was collected and narcotized with CO<sub>2</sub>. After thoroughly removing the mealybugs we placed the ants at a suitable site with numerous *Piper aduncum* bushes. Overlooked mealybugs were taken away during the following controls. A few hours after release the ants began to establish a trail system in the manner mentioned above. A highly explorative behavior led to the formation of up to six trails into the surrounding vegetation. The ants ventured to the very tips of the branches where they formed shortlived assemblies of up to 10 ants. The trail system changed permanently. Eight hours after the beginning of the experiment the ants had found several extrafloral nectaries on a locally abundant *Vitis* sp. (Rubiaceae). These nectaries were visited intensively until the end of the experiment despite their very low nectar production. Only a small portion of the *Vitis* plants could be utilized, however, because the nectaries were mostly occupied by a small *Cremastogaster* species. This ant attacked *D. cuspidatus* immediately in a mass alarm and chased it away with the help of a repellent secretion exuded from its sting.

In addition to the nectaries, *D. cuspidatus* took possession of a few membracid larvae on the *Piper*

bushes. During the whole observation time of 17 days the colony moved some 15 m further on and established a trail system of about 30 m while the number of the workers had greatly diminished. Only pupae and several old larvae were present in the colony. After 17 days there remained only the queen, some nearly mature pupae, and a few hundred of the original 10000 workers. The experiment was stopped at this stage. The colony was offered some *M. formicarii* which were accepted immediately and transported to a *Piper* bush. The extrafloral nectaries of the *Vitis* plants were abandoned within a few hours and the colony disappeared into the vegetation. These observations indicate that *D. cuspidatus* cannot exist without their mealybugs and thus support the obligatory symbiosis hypothesis.

*Mealybugs without ants.* Small and medium *M. formicarii* were taken away from the ants and brought to fresh shoots of *Piper* in the laboratory and in the field. In experiment 1 (Table 6) fresh *Piper* sprouts in narrow-necked bottles were offered to the mealybugs in the laboratory. The plants were carefully preserved in a fresh state by trimming their stems. At the beginning the mealybugs walked around for hours without any feeding or gathering behavior. Later, shortlived assemblies were formed in which some animals produced very large drops of honeydew (Fig. 2) which accumulated in their anal bristles. As these drops were not removed by *D. cuspidatus* as usual, they fell into the mealybug assemblies contaminating and killing some animals. In the course of the experiment an increasing number of mealybugs left the food plant or fell from it and died on the ground, possibly due to starvation. After 3 days most animals had abandoned the plant. A small number were still actively sucking, which proved that the plants were still in a satisfactory state.

In experiment 2 (Table 6) mealybugs were brought to a *Piper* bush in the field. A sticky tape around the stem prevented ants from visiting this plant. These mealybugs moved about without assembling and fell to the ground as time elapsed. Twenty-four hours later all the mealybugs had disappeared, although no predator had been detected. In experiments 3–5 (Table 6) we placed small groups of mealybugs on different *Piper* shoots in the field, which were frequented by other ant species. These were associated with membracids and coccids. Surprisingly *M. formicarii* was not accepted as a trophobiosis partner by these ant species, not even by a *Dolichoderus* sp. Instead they were attacked and carried into the nest either as

**Table 6.** Small and medium larvae of *Malaicoccus formicarii* were released under various conditions in groups on fresh shoots of *Piper aduncum* and observed for 1–3 days

Experiment	Number of larvae per experiment	Number of live mealybugs after 5 h	Number of live mealybugs after 1 day	Number of live mealybugs after 3 days	Cause of death	Remarks
1 In the laboratory on <i>Piper</i> shoots	150	150	131	17	Wandered away, fallen to the ground, contaminated with honeydew	—
2 In the field on an antless <i>Piper</i> bush	100	54	0	0	Wandered away, fallen to the ground	—
3 In the field on <i>Piper</i> with <i>Cremastogaster</i> sp. A	135 50	27 6	0 0	0 0	Fallen prey to <i>Cremastogaster</i> sp. A	Cares for membracids on <i>Piper</i>
4 In the field on <i>Piper</i> with <i>Cremastogaster</i> sp. B	150 53	17 5	0 0	0 0	Fallen prey to <i>Cremastogaster</i> sp. B	Cares for membracids on <i>Piper</i>
5 In the field on <i>Piper</i> with <i>Dolichoderus</i> sp.	200 80	115 5	0 0	0 0	Fallen prey to <i>Dolichoderus</i> sp.	Cares for coccids on <i>Piper</i>

live or dead prey. The *Cremastogaster* species even recruited additional workers to collect this prey. Apparently *M. formicarii* is also unable to survive without its partner.

## Discussion

**Nutrition.** The basis of the symbiosis of *D. cuspidatus* and *Malaicoccus* is the honeydew. This obvious fact is discussed here because Reyne (1954) reported that *Hippeococcus*, which is closely related to *Malaicoccus*, does not provide honeydew for its ant partner, *D. gibbifer*. It is most likely a misinterpretation because he saw droplets at the body end of these mealybugs.

It is important that *Malaicoccus* does not need any kind of mechanical stimulus to excrete honeydew. It is released spontaneously as long as the mealybugs feed. This spontaneous excretion contrasts with other cases of trophobiosis (review in Way 1963) where release of the honeydew is stimulated by the touch of the ants. When visited by ants regularly, they do not squirt it away but store it for some time in their gut. The signal-triggered release of honeydew was obviously developed as a biological necessity, where the ants are not permanently present but only come from time to time. In these cases spontaneous release would have several disadvantages such as the loss of carbohydrates for the ants on the one side and killing or impairing of conspecifics due to agglutination with honeydew on the other side. Excessive honeydew may also attract competitors. In *Malaicoccus*, how-

ever, the constant presence of a large number of ants guarantees that the honeydew which collects between the long bristles at the anus of the mealybugs is removed immediately. It remains obscure why the ants only transport the honeydew to the colony during a few hours of the day. As the storage capacity of the ant crop is limited, the mealybugs must imbibe the phloem sap only at certain times of the day. Perhaps they only feed during the main assimilation time of the plants.

Some intensive honeydew-collecting species like *Lasius fuliginosus* or *Oecophylla longinoda* (Hölldobler and Wilson 1978) supplement their diet with animal protein. As *D. cuspidatus* was never observed to hunt or to collect dead animals under natural conditions, the question arises from which source *D. cuspidatus* obtains its proteins. We cannot yet answer this question definitely. The amino acids in the honeydew perhaps suffice for its nutrition, although in the literature uncertainty exists (Way 1963) about this possibility. Especially for *D. cuspidatus* this seems probable because their mealybugs feed exclusively on the phloem sap in young and growing parts of plants, which is rich in amino acids (Way 1963). It also seems possible that surplus mealybugs are eaten by the ants as shown in *Lasius flavus* (Pontin 1978) although this could not be proved for *D. cuspidatus*. In any case the mealybug population size within the *D. cuspidatus* colony has to be regulated. Besides possibly being utilized as food, surplus *Malaicoccus* could simply be eliminated from the colony. Such killing and ejection of plant lice was recorded for *Oeco-*

*phylla longinoda* (Way 1954). We observed similar behavior in a Malayan *Camponotus* species and in another *Dolichoderus* species which, however, has a completely different mode of life.

The observed feeding on mammal urine is quite common for other rain forest formicids with a honeydew diet. The gathering of bird faeces can also be observed in such ants. Other insects of this region which likewise feed on a plant sap diet such as butterflies or various bees also collect mammal urine and sweat. Possibly they obtain additional electrolytes in this wet forest region deficient in salts. It is unclear whether *D. cuspidatus* is able to utilize the nitrogen in such metabolic end products because no endosymbionts capable of utilizing these substances are known so far.

There may be several reasons why the mealybugs suck exclusively on young plant tissues. As already mentioned the phloem sap of growing plants is especially quantitatively and qualitatively rich in amino acids. Apart from the amino acid rich phloem sap of growing plant parts due to their lack of lignification, they can easily be penetrated by the short beaks of the mealybugs. It is also known that poisonous and repellent secondary plant substances are mainly produced in older plant parts (Luckner 1969). Possibly because of this the polyphagous mealybugs can feed on plants which would normally be poisonous or unpalatable.

The great mutual dependence of *D. cuspidatus* and *Malaicoccus* became most obvious when we isolated the two species. The ants showed an extremely high activity without their mealybugs and soon starved to death. The isolated mealybugs also moved about restlessly and soon died. Under field conditions they quickly fell prey to other ants including species which mainly live trophobiotically, e.g. a *Dolichoderus* sp. It is unclear whether they lack a recognition characteristic for trophobionts or because their restless behavior obstructed their recognition as trophobiotic partners.

Decisive for the comprehension of the sociobiology of *D. cuspidatus* is the frequent change of feeding sites of their mealybugs. Causes and advantages are obvious. As the mealybugs suck on freshly growing plant parts the ants regularly have to search for new food plants which are just shooting, blooming or fruiting. Shifting from one plant to another is easily possible, as the mealybugs are extremely polyphagous. The wide food tolerance of the pseudococcids enables the ants to utilize a wide food niche. The carrying behavior in combination with the mass recruitment system and the high colony mobility of the ants ensures optimal exploitation of the food plants.

*Carrying behavior and colonization of feeding sites.* The frequent carrying of the mealybugs by the ants is very conspicuous. This feature distinguishes *D. cuspidatus* from most of the other trophobiotic ants. Only some other *Dolichoderus* species transport their partners as frequently. The neighboring genus of *Malaicoccus*, *Hippeococcus*, is actively carried by their *D. (Hypoclinea) gibbifer* partner when disturbed (Reyne 1954). These mealybugs often actively climb on their ant partners and are not removed as in *Malaicoccus* by their ants but carried away in this way. In *D. cuspidatus* transport of the mealybugs can be observed in various situations, while shifting feeding sites, during nest change, upon disturbance and even without any apparent cause. At first sight the spontaneous transport of mealybugs in stationary colonies seems to be implausible. It is, however, an absolutely normal feature – on average 11% of the ants on the trails carry mealybugs. This carrying behavior could possibly have regulatory significance. The mealybugs in the nest possibly form a reservoir for times of increased nutritional demand. Obviously, the mealybugs in the nest have to be exchanged from time to time in order to feed, which is not possible in the nest. A permanent fluctuation is also brought about by the constantly changing trophic conditions at the feeding sites. The adult female mealybugs which are indispensable for reproduction are mainly kept in the nest, which is the best protected site of the colony. Mealybugs in the nest interior in “waiting position” were also observed in *Hippeococcus* (Reyne 1954) and *Eumyrmococcus* (Flanders 1957; own observations). However, their host ants are not known to be nomadic.

For colonization of new plants the ants form new trails and move to the apical parts of the vegetation to deliver a few mealybugs. It is not yet known whether the ants recognize young shoots by themselves or just set up feeding sites where the mealybugs begin to suck. Lack of food is one of the factors that stimulates searching behavior of the ants, which was observed in colonies deprived of their mealybugs.

*Migration and nesting behavior.* The mobility of the symbiotic community is decisively enhanced by the constant nest-changing motivation of the ants. Upon a large-scale change of feeding site the whole colony moves in a well organized manner to the vicinity of the new feeding sites.

*D. cuspidatus* represents the first true nomad known in the animal kingdom. Its nomadic behavior resembles the migratory behavior of the army ants (re-

view: Gotwald 1982). However, in contrast to *Ecton* (Schneirla 1971) *D. cuspidatus* lacks the precise rhythmic moving behavior which is correlated with cyclic brood development. *Dolichoderus cuspidatus* simply moves when the food conditions require a change of nesting site. Similarities with the army ants can also be observed in the nesting behavior. In both cases the nesting site is not or to a negligible extent altered by constructive measures. In some army ants the nest consists of a cluster of workers enclosing the queen and the brood. The same is true for *D. cuspidatus*, except that in addition mealybugs are found in the interior. The nesting site requirements also demonstrate the extreme nomadic adaptability of *D. cuspidatus*. Neither height nor substrate decisively determine the position of the nest.

*Colony multiplication.* The ergatoid form of the queens indicates that colony foundation is not initiated by single females. The queen is not much bigger than the workers and has nearly no nutritional reserves. Moreover, solitary colony foundation is made virtually impossible by the fact that to ensure successful nest multiplication, the mealybugs not only have to be carried along by the queen during her search for growing plant parts, but also have to be adequately tended on the exposed feeding plant as well. Therefore, the observed nest budding seems to be the only feasible way of colony multiplication and continuation of the symbiosis. For *Acropyga* (Bünzli 1935) and *Cladomyrma* (Roepke 1930) is known that the continuation of the trophobiosis depends on the queens carrying along their root-sucking coccids during the mating flight and founding their colonies subterraneously and fully claustrially.

*Dolichoderus cuspidatus* has no fixed seasonal pattern of reproduction, as shown by our observations of males in the rainy and dry seasons. The number of young queens remains unknown. The mode of colony multiplication indicates that this number is small. However, one colony produces at least several hundred winged males. This means that our nomadic *D. cuspidatus* resembles the dorylines in their manner of colony multiplication.

*Malaicoccus, partner of Polyrhachis?* The relationship between *D. cuspidatus* and *Malaicoccus* is very close. The partners are interdependent and thus apparently not viable on their own. Takahashi (1950, 1951), however, reported that *M. riouwensis* and *M. formicarii* are associated with *Polyrhachis* (Camponotinae). Presumably this is an error. First, *D. cuspidatus* highly resembles some *Polyrhachis*

*sp.* because of its spines and therefore can be mistaken for *Polyrhachis*. Second, Takahashi describes in both species big and permanent associations typical of *D. cuspidatus*/*Malaicoccus*. As the colonies of most *Polyrhachis* species usually number less than 100 workers, it is almost impossible that assemblies of such size occur.

*Comparative and evolutionary considerations.* *Dolichoderus cuspidatus* and *Malaicoccus* were always found to be associated over the entire Malayan Peninsula. Additional trophobiotic partnerships of *D. cuspidatus* with other homopterans, which were occasionally found, were not maintained permanently. These facts indicate an obligatory symbiosis at least for the region investigated. Close trophobiosis are also known for other ants which can even partly transport their homopteran partners, e.g. *Lasius*, *Acropyga*, or *Oecophylla*. These ants, however, are not specialized on a group of closely related partner species. The subterranean *Lasius flavus*, for example, can be associated with many species of root aphids from different genera, who can also live with other ant partners or even independently (Zwölfer 1958). *Acropyga*, the most renowned example of an ant genus very closely associated with coccids, e.g., *Acropyga paramaribensis*, is associated with coccids of three genera, which are all carried along during mating flight (Bünzli 1935). Whether *A. fuhrmanni* exclusively tends *Eumyrmococcus smithi* is doubtful (Flanders 1957).

All earlier research work dealing with the symbiosis of *Dolichoderus*/*Malaicoccus* has dealt mostly with the mealybug partners. The associated ants were only briefly mentioned and mostly not identified at the species level. Williams (1978) was occupied with a thorough monographic systematic study of *Malaicoccus*. All described species of *Malaicoccus* are very similar and mostly only differ in the number and the length of the body hairs. Our enhanced knowledge on the trophobiotic system raises the question of the species status of these forms. As males have never been found, an exclusively parthenogenetic reproduction is probable. In this case one could speak of morphospecies or a whole complex of diverging local varieties. The described *Malaicoccus* species partly occur close to one another and partly are associated with the same ant species. *Dolichoderus cuspidatus* which was found over the whole Malayan Peninsula does not discriminate between the various *Malaicoccus* species. When a colony in Gombak associated with *M. formicarii* was offered a *M. moundi* from the Genting Highlands it was accepted immediately and carried away. Therefore, it is likely that during territorial fighting or colony extinction an ex-

change of *Malaicoccus* takes place not only between *D. cuspidatus* and its various mealybugs but also between mealybugs of *D. tuberifer* and *D. cuspidatus* which are sympatric in the Gombak and Genting region. In our opinion it would be expedient to study further the problem of speciation in *Malaicoccus*.

Three further similar genera, *Allomyrmococcus*, *Paramyrmococcus* and *Hippeococcus* were combined with *Malaicoccus* by Williams (1978) in the tribe Allomyrmococcini. As far as described all Allomyrmococcini, with the exception of some *Malaicoccus* species, live in partnership with *Hypoelinea* species, a subgenus of *Dolichoderus*. *Dolichoderus cuspidatus* belongs to the subgenus *Diabolus*. From the exclusive symbiosis of the four pseudococcine genera and the two *Dolichoderus* subgenera one may conclude a long coevolution of these insect taxa. The few known details of the biology of *Hypoelinea gibberifer* which is associated with *Hippeococcus* sp. indicates that this symbiosis is also very close and resembles that of *D. cuspidatus*/*Malaicoccus* in some features.

However, our first results from a *Hypoelinea*/*Malaicoccus* system already raise doubts about a long coevolution. In the Genting Highlands we found *H. tuberifer* associated with *M. khooi*. *H. tuberifer* is partly sympatric with *D. cuspidatus* in this mountainous region. This symbiosis seems to resemble *D. cuspidatus*/*Malaicoccus* strongly. Here too mealybugs were carried even if not so readily. The nest structure of this ant was similar to that of *D. cuspidatus* and we also found mealybugs in the nest interior. We also witnessed spontaneous nest-moving, but observed that this species also carried membracids. In the Maxwell Hills some 200 km northwest of Genting Highlands we found *H. tuberifer* not associated with *Malaicoccus* but solely with membracids. Whether this *Hypoelinea* population lost its mealybugs secondarily or never possessed them remains unclear.

The symbiosis between *D. cuspidatus* and *Malaicoccus* is a completely novel mode of life. It has evolved into a sophisticated combination of behavioral features of both partners and is adapted to exploit the high floral species diversity of the tropical rain forest in a unique manner.

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