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Silk Pavilions of Two Camponotus (Karavaievia) Species from Malaysia: Description of a New Nesting Type in Ants (Formicidae: Formicinae)

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Abstract

The nest construction behaviour of two new Camponotus (Karavaievia) species from Malaysia, which were described by DUMPERT (1985) as C. texens and C. gombaki, were examined. Both species weave silk nests, which are attached under leaves in the case of C. texens and between leaves in the case of C. gombaki. While C. texens regularly houses scale insects in its pavilions, single scale insects were found in only 3 out of 94 C. gombaki pavilions. The pavilions of C. texens have as a rule one chamber, those of C. gombaki often have several.

Both Camponotus species weave their nests with the help of last instar larvae. The weaving behaviour of C. texens was examined by the evaluation of films. The weaver larvae, held by the antennae near the front end of their bodies and mechanically stimulated by their antennae, make swinging movements with their front end as they expel their silk. During the weaving sand particles, detritus and bits of plants are fetched by other larvae and built into the silk layer. A third group of larvae works on the as yet loose silk and in this way is responsible for the relatively smooth and firm surface of the finished web. Cooperative leaf pulling during nest construction was not observed. As far as observations were possible, they revealed no difference in the nest construction behaviour of C. texens and C. gombaki. Whether cooperation occurs in C. gombaki could not be elucidated.

Scale insects are carried into the finished pavilions by the texens larvae. They are taken from pavilions with a high density of scale insects. Laboratory observations in which scale insects were pulled by the larvae from leaves outside of the pavilions and thrown to the ground speak for a regulation of the density of the scale insect population. In Malaysia no scale insects were found on the nest tree outside the pavilions. Apart from C. texens no other ants were found on the nest tree. C. gombaki, on the other hand, inhabited the nest tree together with ants of the genera Polyrhachis, Tetraponera, Cataulacus, and Echinopla.

1) Dedicated to Professor Dr. D. SCHNEIDER on his 65th birthday.

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While the manner of nesting of Camponotus gombaki is similar to that of Polyrhachis, Camponotus texensis represents a new type of weaver ant. Its territory is dominated by one-chamber pavilions. It usually houses scale insects inside the pavilions and is as highly differentiated in its nest building behaviour as Oecophylla but in a different manner.

Introduction

While searching for arboricole ants in a Malaysian rain forest we came across a striking Camponotus species. The undersides of many leaves of a 7 m high tree were covered with pavilions. When we struck the branches of the tree a rustling sound could be heard and a great number of ants, approximately 5 mm long, plunged out of the pavilions, immediately attacking us with bites and the expulsion of formic acid. In the opened pavilions we discovered brood and numerous scale insects as well as adult ants. The walls of the pavilions were of a silk-like material over which was a dense crust of fine particles. The pavilions of a second Camponotus species, very similar to the first, were composed of leaves woven together and laid over one another; these contained no scale insects. The silk-like building material led us to suppose that we were dealing with two unknown species of weaver ants. We therefore examined the construction of the nests more closely.

Material and Methods

The field observations were mainly carried out in February 1984. A total of two colonies of the first Camponotus species (A) were found: one in Gombak Valley, approximately 25 km north of Kuala Lumpur, the other at Kuantan, on the east coast of Malaysia. Both colonies lived in lightly disturbed rain forests at a height of 500 and 100 m respectively. Only one single colony of the second Camponotus species (B) was found. This colony was nesting in two trees of the same type standing together directly on the edge of a road in the Gombak Valley.

The nests of species A from the vicinity of Kuantan and all of the pavilions of the species B on one of the two trees were examined more closely. The inhabitants, 250–300 ♂♀, one ♀ and brood of the species A and 100–150 ♂♀ with a little brood of the species B were taken back to Germany. They were placed in terrariums (100 × 100 × 40 cm) in which Ficus benjamini (with scale insects from the greenhouse), Ficus spec. and Passiflora spec. were cultivated in flower-pots. The lighting and heating were provided by a Flora set lamp (Osram, HGL — R 88 W de Lux) in each case. A time switch provided a 12 h day from 7.00 to 19.00 h. A temperature of 25–30°C was maintained. By regular spraying of the plants a humidity of at least 90% could be maintained. Cockroaches cut into small pieces, Tenebrio larvae and flies were accepted by the ♀♀ of both species as food.

The weaving behaviour was analysed more exactly with the help of a Super-8 film (Beaulieu B 4008 — ZMII) on Agfa Chrome CT 18 and evaluated with a single frame viewer. The film speed was 18 frames/s. A binocular was used for the observations in the terrarium.

Results

1. Systematic Position

Both Camponotus species (A and B) belong to the subgenus Karavaievia (Emery 1925), from which two species and one subspecies have hitherto been
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specified. All come from the Indo-Malaysian area: *Camponotus exsectus* Emery 1901, *C. dolichoderoides* Forel 1911 and *C. dolichoderoides* var. *overbecki* Viehmeyer 1915. The species examined by us are distinctly different from those already known and were described by DUMPERT (1985). *Camponotus* A has been given the name *Camponotus texens*, *Camponotus* B the name *Camponotus gombaki*.

2. Description of the Nests

Despite intensive searching in various regions of West Malaysia over a total of 7 months, no more than 2 colonies of *Camponotus texens* and only one single colony of *Camponotus gombaki* were found. Thus both *Camponotus* species seem to be rare in the area of examination; the numerous pavilions of *Camponotus texens* under leaves are not very difficult to recognize.

The colony of *Camponotus texens* in Gombak Valley built a total of 207 pavilions, mostly restricted to the lower part of the tree, with only 5 nests in the uppermost regions. Although several neighbouring trees stood in direct contact with the nest tree, almost none were colonized. Only 5 pavilions were found on a neighbouring large-leaved tree. Two contained a few (< 10) but none housed scale insects. In 1983 two neighbouring trees, a rattan palm on the nest tree and a creeper were colonized with 5, 1, 1, and 6 pavilions, respectively, 3 of them with and 10 without pavilions. Apart from the pavilions of *Camponotus texens* we found no other ants on the nest tree. The ants wove over the hollow step of an aluminium ladder over a period of 4 weeks, without transporting brood into the resulting nest.

The number of pavilions per branch of the nesting tree varied between 1 and 50 and was, in part, in accordance with the size of the branches. 350 leaves were counted on a particularly densely colonized branch in the lower part of the nesting tree, 66 (approx. 19%) carrying pavilions. All of the nests were woven on older leaves, none on young fresh leaves. 10% of the pavilions were found between leaves — both living and dead ones — and 90% under leaves. All of the pavilions of the nesting tree inhabited by ants \( n = 50 \) housed scale insects, of which the larger ones were to be found on middle ribs, the smaller ones mostly on side ribs. No scale insects were found outside the pavilions. The colour of the leaves was lightened at the points where the pavilions were placed. In 9 examined pavilions there were, on average, \( 13 \pm 8 \) \( \sigma \), \( 17 \pm 9 \) large and \( 17 \pm 10 \) small scale insects. In 7 out of 50 pavilions there were \( 1-12 \) \( \delta \). In 2 out of 50 pavilions we found 2 \( \delta \), one winged, the other unwinged. In the previous year winged females and males were found at the same time of the year in this colony. 5 out of 9 pavilions housed ant larvae, the number of which varied from 1 to 56. Two types of nests could be differentiated: one contained a few large larvae — presumably weaver larvae —, the other also held small larvae and probably served as a brooding pavilion.

The second colony of *Camponotus texens* from the Kuantan area was found on a large *Uncaria* tendril, a ligneous creeper common there. The
pavilions were attached both on the undersides of leaves and between leaves, to tendrils and to the stalks of leaves. The scale insects sat on the leaf ribs and on twigs. Over 50 pavilions were counted but the leaf pavilions only rarely housed scale insects. The pavilions were not opened to count the inhabitants on the spot because of heavy rainfall. Rather they were all removed with the leaves, tendrils and twigs on which they were fastened and transported to Germany. The count showed that the colony consisted of 250—300 ♀️, 1 ♂️, brood, approx. 20 winged ♂️♂️, and 8 ♂️♂️.

The colony of *Camponotus gombaki* was situated on 2 trees of the same species, standing next to each other. One of these was felled on 15-2-1984 and 94 pavilions secured. As the same number of nests was probably to be found on the second nest tree, the number of pavilions of this colony was estimated at about 200. All pavilions were woven between leaves, one of which was always a living leaf, the other either a living or dead one. A loss of chlorophyll from the leaves in the nest area, regularly observed with *Camponotus texens*, did not occur in the case of *Camponotus gombaki*. 15 pavilions which were inspected contained an average of $19 \pm 14$ (♂️♀️). About half of these pavilions housed brood: 1—10 larvae and up to 60 pupae. In the case of approx. 25% of the examined pavilions a species of spider was found, which had spun its web near the entrance of the nest.

Most of the pavilions on the felled nest tree were situated in the lower regions. The upper top region of the tree, which had 22 branches, carried a total of 6 pavilions, of which 3 were not colonized. The lower top region carried 5 nests, all of which were colonized. In the middle region there were 30 nests on a total of 7 branches and in the lower region of the tree 53 nests. Only 2 of these 94 pavilions contained single scale insects of various species. A fertile queen and young sexuals were not found in the pavilions. Apart from the ♀️♀️ of *Camponotus gombaki* ants of the genera *Tetraponera*, *Cataulacus*, *Echinopla*, and *Polyrhachis* were found on the nest tree.

The pavilions of *Camponotus texens* were composed as a rule of an unbranched pocket of silk, over-layered with particles (Fig. 1). This pocket was fastened over the middle rib on the underside of the leaf and covered approx. a third of the leaf surface. Some pavilions (approx. 20%) were not woven under but between leaves. In one case 2 neighbouring pavilions stretched over 4 leaves. A further type of pavilions was woven between forked branches like a tent or else it enclosed a branch and the leaf stalk to be found on it. 18 out of 25 pavilions examined had one entrance, the other 7 two entrances.

*Fig. 1: Pavilion of Camponotus texens and ♀️ at its entrance*
The pavilions of *Camponotus texens* were, as a rule, fully covered on the inside with a thin but dense layer of silk. The roof appeared to be white on the inside and all of the particles imbedded there were carefully woven over with silk. The floor, that is the upper surface of the leaf, was also laid out with silk in 14 out of 18 pavilions. In 4 pavilions this floor covering stretched along the fastening points and only fragmentarily over the surface of the leaves.

The pavilions of *Camponotus gombaki* did not consist of a free-hanging pocket on the underside of the leaves, but lay either inside rolled leaves or between two or more leaves laid one over the other (Fig. 2). The seams were fastened with silk, on which particles were sometimes also laid. 30 out of 38 pavilions were woven between 2 leaves, 4 pavilions on 1 leaf and again 4 pavilions between more than 2 leaves. The nests were often divided into several chambers which, according to our observations, arose through the building of further chambers onto existing nests. The number of entrances varied from 1 to 4: 4 out of 8 pavilions had 2 entrances, 2 only 1, 1 had 3 and one 4. In 16 out of 26 pavilions the covering of the pavilions with silk extended over the upper and lower sides. In 10 pavilions only one side was covered with silk.

![Fig. 2: Pavilion of *Camponotus gombaki* which is woven between leaves](image)

The structure of the woven nests of *Camponotus texens* and *C. gombaki* was — for comparison with *Oecophylla* nests — examined with a SE-microscope (Fig. 3). This figure shows that the silk parts of *Oecophylla smaragdina* nests are considerably more densely and uniformly woven than those from *Camponotus texens* and *C. gombaki*, which differ little from each other. The threads of the *Oecophylla* nests and those of the *Camponotus* nests are netted and branched. Their thickness is 1—4 \(\mu m\) for *Oecophylla* and 0.1—1.2 \(\mu m\) for *Camponotus*.

In the laboratory we counted the ants leaving the pavilions and arriving at them during the day and at night. We found that the maximum of the
activity of both *Camponotus* species could be observed during dusk and dawn. When foraging the ants not only accepted honeydew from scale insects but also pieces of insects (cockroaches and *Tenebrio* larvae) which we offered them. In addition, *Camponotus gombaki* captured small Diptera as prey.

3. Nest Construction and Weaving Behaviour

*Camponotus texens* and *C. gombaki* build their silk nests with the help of their larvae. This was shown by direct observations, photos and — in the case of *C. texens* — by the evaluation of film made at the laboratory colony. These displayed clearly that the larvae are held during the weaving process.
by the ♀♀ near the front end of their bodies and are regularly touched by the ♀♀'s antennae on their heads and foremost parts of their bodies. The larvae then carried out 38—40 movements per min back and forth with the foremost part of their bodies. This part of their bodies was so flexible that they were able to bend their heads back to the middle of their bodies. If the head of the larva touched solid substrate it dapped at it once or twice quickly with its labium and only then would it raise its head again. 70 ± 4 contacts of the head of the larvae with the floor of the nests were counted per min for 5 larvae. During this time the expulsion of silk could be observed (Fig. 4). The larvae made frequent movements to the side with the foremost part of their bodies both as they raised themselves up and as they dapped at the substrate. For surface weaving, which served for example to cover the floor of the nest, the larvae held by the ♀♀ lay on the surface of the leaves. The larvae, stimulated by the ♀♀ to spin, raised the foremost part of their bodies seldom and then only a little, but dapped with their heads quickly and repeatedly at the substrate and moved the foremost part of their bodies at the same time to and fro.

The larvae used for nest construction (weaver larvae) were all in the last instar. The relation between the size of the weaver larvae and the size of the

![Image](image_url)

*Fig. 4: ♀♀ of Camponotus texens (a) and Camponotus gombaki (b) weaving with larvae*
weaving \( \frac{3}{8} \) was on average 0.85, so that the weaver larvae reached about \( \frac{6}{7} \) of the size of the \( \frac{3}{8} \) weavers with them. The colony of *Camponotus texens* observed in the laboratory did not use all of their last instar larvae for weaving.

\( \frac{3}{8} \) of every size functioned as weavers, including those no bigger than their larvae and young which were not fully coloured. The evaluation of the films showed that the weaving \( \frac{3}{8} \) touched the head and foremost part of the body of the larvae 3 to 7 times, often only with one antenna, while the other antenna controlled the silk or the substrate being woven (Fig. 5). If the \( \frac{3}{8} \) interrupted antennal contact with the larva it displayed spinning movements for approx. 1/2 min and then stopped altogether. Larvae laid on the silk after weaving usually became immediately quiet. We rarely observed larvae which continued to make spinning movements and expel silk 2—3 min after being laid on the web. These larvae were very plump and probably close to pupating.

Fig. 5: Sequence of the weaving behaviour of *Camponotus texens* drawn from a Super-8 film and a single frame viewer

Shortly after the spinning of the first silk strands small particles of sand, detritus and pieces from plants were brought by other \( \frac{3}{8} \) and built into the layer of silk which was as yet thin. For one weaving \( \frac{3}{8} \) and her larva there were usually 2 \( \frac{3}{8} \) fetching particles; these did not differ from weaving \( \frac{3}{8} \) with respect to size and age. The particles were mostly gathered from the ground at a distance of up to 0.5 m from the nest, but were also bitten off the trunk of the nest tree. Nest material from deserted or half-finished pavilions was disassembled and the silk with particles attached was built into the new nests. From neighbouring inhabited pavilions only particles without silk
were removed. The fastening of the particles in the silk strands, which took place with the help of "screwing" movements of the head and by pushing with the forelegs, was only begun after an examination of the web with the antennae.

Apart from the weavers and the particle carriers further 8Y helped to make up the "construction team". There were 2 to 5 times more of them than particle carriers. They bit into the loose silk, especially at the points of connection with the leaf surface, and pushed together. In this way the relatively smooth and firm surface of the finished web was attained.

The construction of a new pavilion usually began with an assembly of 8Y for several days at the spot where the building of the nest was to take place. However pavilions were also begun on leaves of the Ficus benjamini infested with scale insects without this assembly phase. Here construction started when a 8Y took a weaver larva from a nest and began to weave with it. After a short time other 8Y followed and brought in one or two further larvae. Shortly after the start of the weaving the transport of particles and the forming of the silk began. For the weaving of big free silk areas, the silk layer was extended from the borders concentrically until the hole in the middle could be woven in, somewhat similarly to the shape of an iris. Towards the end of the construction of the pavilion some 8Y began carrying scale insects into it.

The exact observations of weaving behaviour described here were mainly gained by observation of Camponotus texens, as the weaving of C. gombaki could not be filmed. The colony of C. gombaki had no queen; it weaved only for a short time and then at points which were difficult to observe. In so far as observations were possible there is no difference in the nest construction behaviour between C. texens and C. gombaki. However cooperation of particle carriers and other assistants during nest building was not observed in C. gombaki, so this behaviour could neither be confirmed nor denied in this species.

4. Scale Insects in the Nests

The 2 colonies of C. texens tended two different coccid species. The scale insects offered to the ants in the laboratory were not of the same species as those at their disposal in Malaysia. Both of the Camponotus species accepted the scale insects in the laboratory as trophobiosis partners. Scale insects sitting freely on the nesting tree in the laboratory were tended both by C. gombaki and, for a short time, by C. texens.

When C. texens began to build pavilions in the laboratory, scales were taken from the tree and transported into the interior of the new nests. Later on new pavilions were populated with scales from open sites of the tree as well as from existing pavilions. The transport of scale insects into the pavilions was observed 159 times, conducted by 25 different 8Y. Mainly small, mobile scales were transported, but a few big scale insects as large as an ant's head in diameter were also moved. After they had been deposited in the nest, the scale
insects scurried around, then mostly lodged themselves firmly on the middle rib and other ribs of the leaf. During nest movements the scale insects were observed being carried from an old to a new nest of the *texens* colony.

Laboratory observations show clearly that the number of scale insects is regulated by *Camponotus texens*. After establishing the pavilions, the ants began to display aggressive behaviour against scales sitting freely on the nest tree. After making repeated biting movements in the direction of the scales, the ants lifted them and hurled them from the trunk of the *Ficus*. This explains why we could never observe scales outside the pavilions on the nesting plants in the field.

**Discussion**

The habitat of almost all weaver ants is the foliage of tropical forests. Silk-spinning ground nest builders are only known within the genus *Polyrhachis* (Forel 1928; Ofer 1970). This habitat is most likely secondary for them. Construction with the strong and durable silk, which is exceptionally suitable for manipulation, allows the ants to provide themselves with optimal nesting places at any spot in the stratum of bushes and trees lacking in holllows.

Hitherto 2 types of nesting have been described:

(1) Central nest constructions, built by ants with high populations and thus dominating their habitat. They are always divided into many chambers. Examples of these are the nests of *Oecophylla longinoda* and *O. smaragdina* in the paleotropical and papuanic Australian region and the nests of *Camponotus (Myrmobrachys) senex* and *C. (M.) formiciformis* in the neotropical region. Trophobiosis partners may be built over with special silk pavilions.

(2) Nests constructed with only one or a few chambers built by ants, with small colonies not dominating their habitat. The nest constructions of many species of *Polyrhachis* from the paleotropical region may be included here (Hölldobler & Wilson 1983; Maschwitz & Dumpert, unpubl.). Here silk pavilions are not constructed for trophobiosis partners.

The manner of nesting of *Camponotus gombaki* partly corresponds to type (2). On the other hand this *Camponotus* species is, because of its comparatively large population, dominating and aggressive, and constructs numerous branch nests.

*Camponotus texens* represents a new type of weaver ants. It is as dominating and aggressive as *Oecophylla* but it occupies and dominates its territory by different means. Unlike *Oecophylla*, *C. texens* builds numerous one-chamber pavilions which are distributed on the whole nest tree. These pavilions contain trophobionts as a rule and the majority also hold brood. This combination of brood and trophobionts is accomplished by the behaviour of the *z* of *C. texens*. They actively populate the pavilions with brood and scale insects during nest construction. Scale insects are not tolerated outside the pavilions. In this way scales neither come into contact with parasites nor
attract predators or ant competitors. To regulate the scale insect population in the laboratory, surplus coccids on the nest tree were either transported into new pavilions, deposited outside of the nesting area or even thrown to the ground. Possibly under natural conditions surplus scales are eliminated in a similar way. We could not clarify whether or not the ants also eat scale insects.

*Camponotus texens* does not cultivate any specific type of scale insects. It accepted the indigenous scale insects in the Frankfurt greenhouse immediately and kept different species of coccids in the 2 nests found in Malaysia. Its way of cultivating scale insects is by no means self-evident. When we offered *Camponotus gombaki* the same greenhouse scales as *C. texens*, they were not transported into pavilions, neither were surplus insects eliminated from the nest tree or built over with silk pavilions.

*C. texens* and *C. gombaki* increase the number of known *Karavaievia* species from 2 to 4, of which 2 have been recognized as obligatory weaver ants. The slight morphological species difference within the clearly definable subgenus (DUMPERT 1985) suggest that all *Karavaievia* species are weaver ants. Apart from the results presented here, the observations of VIEHMEYER (1915) also indicate this. He observed that the nests of *C. (K.) dolichoderoides var. overbecki* are built under leaves and they therefore possibly correspond to the type which we have found in *C. texens*. *Karavaievia* would be then a second weaving *Camponotus* subgenus from which — as from *Myrmobrachys* of the neotropics — no non-weaving species is known with certainty. The nest constructions of the two subgenera differ distinctly, while the differences within the subgenera are slight (compare for *Myrmobrachys*: SCHREMMER 1979a, b; DUMPERT 1978). In order to gain knowledge of the evolution of the weaving behaviour within the genus *Camponotus* it is important to examine the nests of further *Karavaievia* and *Myrmobrachys* species, to have more exact knowledge of the biogeography of the species and to investigate the nest construction habits of further *Camponotus* subgenera.

The weaving behaviour of the examined *Karavaievia* species corresponds with stage 2 of communal nest weaving after HÖLLODÖBLER & WILSON (1983) and is similar to that of *Camponotus senex*. The *C. texens* and the *C. gombaki* larvae differ from *Dendromyrmex* (WILSON 1981) in that they normally only spin when stimulated by ♂♂. Distinct differences are also found between the behaviour of *Oecophylla* and that of *C. texens* and *C. gombaki* larvae. These two use the mobile front part of their body and therefore take a considerably more active part in weaving than the *Oecophylla* larvae which are restricted to producing silk while the weaving is performed by the ♂♂ alone. *Oecophylla* larvae do not spin cocoons for pupation. This is also true for the larvae of *Polyrhachis* spec., similar to *doddi* (HÖLLODÖBLER & WILSON 1983), while other *Polyrhachis* species we observed in South East Asia produce cocoons. Both *Karavaievia* species spin thin cocoons too. They, however, minimize silk consumption in a different way by using the silk of no longer inhabited old pavilions for the construction of new nests.
Oecophylla appears especially highly developed because of its sophisticated cooperation during nest building. This enables them to construct their central nests at almost any site in the foliage. This type of cooperation could not be found in C. texens and C. gombaki, but they do not need leaf pulling and fixing behaviour because of the small size of their nests. Instead of big central nests they produce small pavilions. In C. texens we could, however, observe that the cooperate in a different but also highly specialized and developed way during nest construction. 4 groups of are found which simultaneously perform different tasks: weavers, fetching and attaching particles in the fresh silk, manipulating the silk and fetching coccids for the new pavilions. This means that C. texens is as highly differentiated in its nest building behaviour as Oecophylla but in a different manner.

Zusammenfassung


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