

Colony structure of a bamboo-dwelling *Tetraponera* sp. (Hymenoptera: Formicidae: Pseudomyrmecinae) from Malaysia

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Summary

The colony structure of the bamboo-inhabiting SE-Asian pseudomyrmecine ant *Tetraponera* sp. PSW-80 near *attenuata* F. Smith was investigated at the Ulu Gombak Field Studies Centre, Selangor, West-Malaysia. Based on the dissection of 54 stem internodes from 12 different culms of the large bamboo *Gigantochloa scortechinii* Gamble and on the mapping of three colonies, the following demographic characteristics emerge. The colonies are monogynous but highly polydomous (at least up to 36 internodes and up to 9 stems occupied) and very populous for a pseudomyrmecine not involved in an ant-plant mutualism. One completely censused colony had 6953 adult workers and 2079 alates (adults plus pupae). The single queen suppresses gyne development in her own "nest" and, to a lesser extent, in other "nests" within the same stem. The overall numerical sex ratio was 0.96:1 (females:males), the investment sex ratio, 2.93:1, i.e., almost exactly the 3:1 ratio expected for a monogynous outbred hymenopteran in which the colony queen also produces all the male offspring. Brood is distributed to all other nest chambers from the queenright chamber. The symbiotic pseudococcids (*Kermicus wroughtoni* Newstead) are present in all inhabited internodes, with small early instar individuals prevailing numerically by far over the larger stages. The rich well secluded honeydew supply within the internode and the efficient architectural protection provided by the internode wall (access usually only through a 2 × 3 mm-hole) allow *T.* sp. PSW-80 to reach an unusually large colony size without being an aggressive and protective plant mutualist like other members of its subfamily with similar demographic features.

Introduction

The Pseudomyrmecinae are a small subfamily of mostly tropical and subtropical ants comprising the Old World genus *Tetraponera* (ca. 100 species) and the New World genera *Pseudomyrmex* (ca. 150–200 species) and *Myrcidris* (monotypic) (Ward, 1991). Almost all species are arboreal and a considerable number have entered into mutualistic associations with myrmecophytes (Janzen, 1966; Ward, 1991). While some data on colony structure have been gathered on *Pseudomyrmex* (Creighton, 1950, 1955; VanPelt, 1958; Janzen, 1967, 1973, 1975; Schremmer, 1984; Ward, 1985;

Klein, 1987 a, b) and African *Tetraponera* (= *Viticicola* = *Pachysima*) (Terron, 1968, 1969, 1970, 1977; Janzen, 1972), nothing is known on the colony structure of any of the Asian species.

At the Gombak Field Studies Centre of the University of Malaya, near Kuala Lumpur, and its immediate vicinity we found five *Tetraponera* species. Three of these, *T. pilosa* (F. Smith), *T. attenuata* F. Smith, and *T. sp.* PSW-72¹, usually inhabit dry twigs in shrubs or trees; the other two, *T. sp.* PSW-80 near *attenuata* F. Smith¹ and *T. allaborans* (Walker) (s.l.)², appear to be confined to living bamboo (unpubl. obs.; A. Schellerich, pers. comm.). While the bamboo-specialists were always found associated with mealybugs, the three dry-twig nesters seem to be comparable in nesting and food requirements to generalized Pseudomyrmecinae, collecting honeydew and nectar from a variety of sources and hunting and scavenging dead arthropods and minuscule organic particles licked up from plant surfaces and consolidated in the infrabuccal pocket (unpubl. obs.; cf. Creighton, 1950; Janzen, 1966; Terron, 1970).

We report here on the larger one of the bamboo-specialists, the shiny black *T. sp.* PSW-80 (= "*Te*") (workers ca. 9–10 mm long). At the Gombak Field Studies Centre we found it only in stem internodes of the large bamboo *Gigantochloa scortechinii* Gamble (height up to 25 m, diameter 8–10 cm, internode length 20–60 cm), but it has also been collected in the more slender *Gigantochloa ligulata* Gamble at Endau Rompin (D. Kovac, pers. comm.) and in a bamboo twig internode at Genting Highlands (U. Maschwitz, unpubl. obs.). *Te* seems to subsist to a large extent on pseudococcids (*Kermicus wroughtoni* Newstead³) that it cultivates within the bamboo stems. It exhibits several unusual behaviors, including ejection of excess water from the internodes (Klein et al., 1993) and carrying of pseudococcid larvae by young queens during the nuptial flight (Klein et al., 1992). Unlike some other ants specialized on a narrow range of plants, it does not protect its host, in that respect being similar to two species of *Polyrhachis* (Formicinae) found at the Gombak Field Studies Centre that are likewise restricted to nesting in bamboo without defending it (Dorow and Maschwitz, 1990).

Because mature *Te*-colonies inhabit clearly delimited cavities (bamboo internodes) that – once an inhabited bamboo stand has been detected – are easily located by searching for the small guarded entrance holes and collected with most of their inhabitants (the workers rarely leave their nests; the small entrance holes can be plugged easily to prevent escape), this species, despite its large colony size and high degree of polydomy, is well suited for an exact determination of its colony structure. Also the numerical relation between the ants and their symbiotic Homoptera in the different internodes can be quantified exactly. All this not only allows the

¹ *T. sp.* PSW-72 (near *allaborans*) and *T. sp.* PSW-80 (near *attenuata*) are code names assigned to undescribed species by Dr. P. S. Ward, University of California at Davis, who is preparing a revision of *Tetraponera*.

² *T. allaborans* s.l. is common in the primary lowland rainforest habitat of Pasoh, Negeri Sembilan, where bamboo is virtually absent (Roszczewski, pers. comm.). We consider it quite likely that the Pasoh-species is a sibling species of the (apparent) bamboo specialist at Gombak.

³ Identified by Dr. G. W. Watson and Dr. D. J. Williams, Natural History Museum, London, but poor condition of the type material precludes absolute certainty on the species identity.

investigation of important sociobiological questions like, for example, the extent of queen control over alate production, but also makes possible a probe into the causes and effects leading to plant specialization in ants. As a first contribution to the sociobiology of *Te* we present and interpret here our census results on one totally and four partially collected colonies from the vicinity of the Ulu Gombak Field Studies Centre.

Materials and methods

Among the numerous *Gigantochloa scortechinii* stands in the vicinity of the Gombak Field Studies Centre eight in an area of about 2 ha near the Gombak river were found to be inhabited by large colonies of *Te*. We selected one colony (BM 1) inhabiting six out of 11 stems of one of these bamboo stands for a complete census. Between 1 and 3 Feb. 1992 the bamboo culms were cut close to the soil surface in the mostly uninhabited first visible internode. The ants stayed inside their internodes despite the disturbance. All entrance holes were closed with insulating tape and a small amount of 70% ethanol was injected into each internode to kill the ants. Then the internodes were opened with a saw and the adult ants, the sexual pupae, and the pseudococids were censused. The numbers of the small first-instar pseudococids were estimated by counting them roughly as groups of five.

Another six inhabited stems representing portions of four of the eight inhabited bamboo stands were collected and censused in March 91, August 91, and March 92 (DK 1, RK 1, RK 2, BM 2).

In the following, internodes are numbered from bottom to top within each stem. Internode # 3–5 refers to the 5th internode above the base of the 3rd stem, internode # 6–1 to the basal internode of the 6th stem, etc. "Inhabited internode", "nest", and "(nest) chamber" are used interchangeably, as are "(bamboo) stem" and "(bamboo) culm".

Results

1. Spatial organization

Figure 1 shows the spatial arrangement of the completely censused colony, BM 1, when collected on 1–3 Feb. 92. The E-exposed bamboo stand covered ca. 4 m² on the steep slope of a ditch. The length of the individual culms was between 14 and 16 m, the height of individual internodes 20–50 cm, their diameter 8–10 cm, and the thickness of their walls 10–15 mm.

Six out of the 11 stems (one of which was dead) were inhabited, with between one and 15 internodes per stem occupied by *Te* adults, brood, and symbiotic pseudococids. A total of 36 internodes with a combined length of 10.96 m and a volume of ca. 70 l was occupied by the ants. The single queen was found in the basal internode of stem # 4. In a second colony (BM 2) we initiated a nest relocation by sawing a hole into an internode about 1.5 m above ground. By chance we hit the chamber

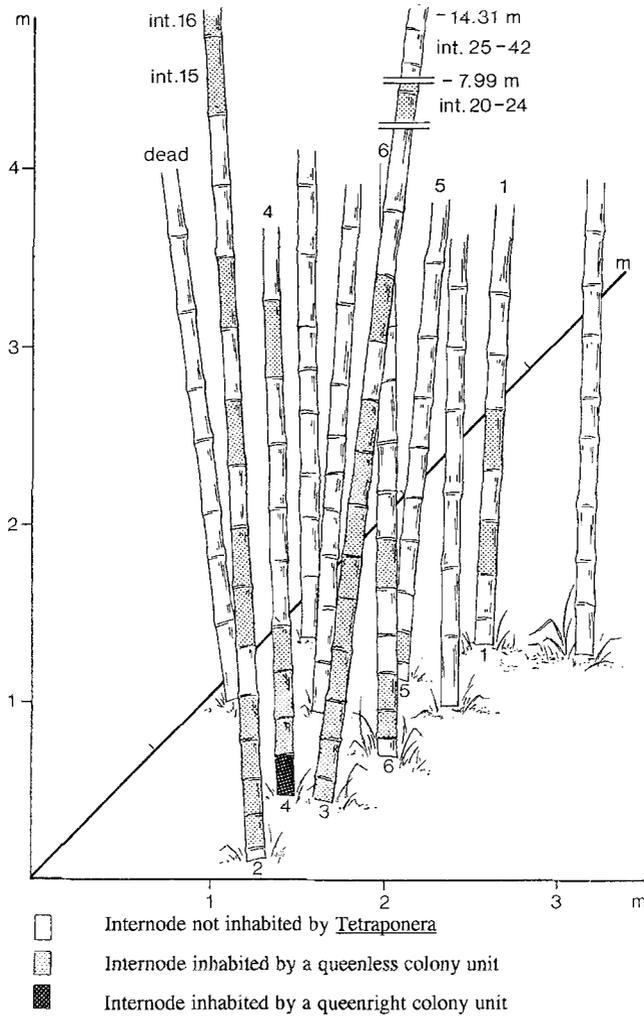


Figure 1. Distribution of a *Tetraoponera* sp. PSW-80 colony (“BM1”) across a stand of *Gigantochloa scortechinii* bamboo. The internodes of the six inhabited culms have been drawn to scale. Cf. Table 1 for population data

containing the queen and watched her being carried to a neighboring inhabited stem. This shows that the queen is not always in an internode close to the ground. The highest inhabited internodes of colony BM 1 were in stem # 3 (internodes # 3–20 to 3–24) at up to 8 m above the ground. One to several uninhabited internodes separated some of the inhabited ones in all stems with more than one nest.

Each inhabited internode had at least one and up to three (in one case five) entrance holes in its wall. No internal connection through the transverse nodal walls was found between adjacent internodes. All traffic between the internodes and stems thus had to take place over the surface of the stems, the ground between them, or

across bridges formed by twigs and leaves of surrounding vegetation. The entrance holes were small, with an oval or slit-like shape (length 2.2 to 5.0 mm; width 1.5 to 1.8 mm ($n = 23$)). They were widened toward the inside to form a cavity in the wall where one to several ants guarded the entrance. According to D. Kovac (pers. comm.) the holes are products of wood-boring insects, usually pyralid larvae, and in some cases, woodpeckers. Internodes lacking a hole are inaccessible to *Te*, and those with wider holes are never inhabited by *Te*.

The culms of two other *Te*-colonized bamboo stands, adjacent to each other, were surveyed extensively in July and August 1991 for *Te*-entrance holes up to a height of ca. 2 m. By chance observations of very sporadically occurring heavy worker traffic additional nest chambers up to ca. 6 m high were located; almost certainly a fair proportion of inhabited internodes higher up remained undetected. The true degree of polydomy therefore was probably considerably higher than indicated by the numbers of nests actually detected.

Colony RK 1, located in a bamboo stand with 35 culms (including 3 dead ones), was found inhabiting 9 culms (7 mature and 2 young ones), delimiting a roughly triangular area of 2.4 m², with together at least 28 internodes (1 to at least 9 internodes per stem); the *Te*-inhabitants of the two young stems were collected and censused.

Colony RK 2, found in a stand with ca. 15 culms (one of them dead), was detected in 4 of them (all mature), delimiting an almost square area of 0.6 m², with together at least 11 inhabited internodes (1 to at least 5 internodes per stem). The *Te*-inhabitants of one stem were collected and censused.

Colonies RK 1 and RK 2 inhabited two neighboring bamboo stands. The closest stems of the two colonies were 7 m apart. Combining several pairs of workers from the two colonies led to fighting to the death; in contrast, workers from the two different stems of colony RK 1, which had been 2.6 m apart in the field, behaved amicably to each other under the same conditions. Eventually, the six collected nests of colony RK 1 and the four nests of colony RK 2 were respectively combined peacefully to form two laboratory colonies.

2. Size and distribution of worker populations

The completely collected colony BM 1 in all had 6953 adult workers and a single slightly physogastric dealate queen which was located in the basal internode (#4-1) of a stem with 5 nest chambers. In addition, there were 2079 young sexuals (adults and pupae combined).

Table 1 (cf. also Fig. 1) reveals the distribution of the colony across the 35 inhabited internodes in the 6 different stems (an additional internode, #3-1, had been accidentally opened; to minimize the loss of colony members we waited overnight until the population of the destroyed internode had moved to other chambers). The largest worker population by far, with 543 individuals, was present in the queenright nest (#4-1). The second largest nest (#2-12) had 425 workers, 5 nests had 300-399 workers, 9 nests had 200-299 workers, 9 nests had 100-199 workers, and the remaining 9 nests had below 100 workers. The three stems with the largest

Table 1. Ant and pseudococcid populations in internodes of *Gigantochloa scortechinii* inhabited by a *Tetraponera* sp. PSW-80 colony ("BM1") collected completely on 1–3 February 1992 (ad – adults; nr – not recorded; pu – pupae; Q – queenright). For spatial distribution of the bamboo stems see Fig. 1

Internode	Workers (ad)	Gynes		Males		Pseudococcids		
		(ad)	(ad + pu)	(ad)	(ad + pu)	large	medium	small
#1–3	143	–	–	5	14	3	1	100
#1–5	77	4	15	1	8	2	–	150
Stem #1	220	4	15	6	22	5	1	250
#2–2	143	25	25	11	20	6	–	90
#2–3	119	14	18	5	15	7	–	120
#2–4	368	35	40	19	48	13	–	90
#2–5	285	24	24	20	52	10	–	130
#2–7	149	8	8	6	28	2	–	80
#2–8	175	3	4	9	29	3	–	90
#2–10	261	50	57	15	36	10	–	50
#2–12	425	106	111	27	77	18	7	120
#2–15	243	45	50	29	55	7	1	160
#2–16	293	70	86	43	64	3	12	110
Stem #2	2461	381	423	184	424	79	20	1040
#3–1*	*	*	*	*	*	5	1	80*
#3–2	393	37	61	39	63	15	–	120
#3–3	386	nr	52	nr	78	16	1	160
#3–4	226	75	76	21	36	7	5	110
#3–5	245	nr	48	nr	76	14	–	80
#3–6	233	10	21	26	61	10	4	40
#3–7	195	nr	54	nr	20	11	1	70
#3–8	192	102	102	24	46	11	1	160
#3–9	126	nr	7	nr	18	2	–	50
#3–11	169	35	38	16	30	4	2	40
#3–20	54	–	–	–	–	–	–	180
#3–21	61	–	–	11	11	–	3	60
#3–22	20	–	–	–	–	–	–	30
#3–23	31	–	–	1	1	–	–	80
#3–24	32	–	–	–	–	–	–	120
Stem #3	2363	nr	470	nr	440	95	18	1380
#4–1Q	543	–	–	–	1	10	2	85
#4–2	308	10	18	34	68	10	1	120
#4–3	188	–	–	31	41	6	5	80
#4–4	243	13	14	25	57	5	4	140
#4–9	202	nr	19	nr	42	4	1	150
St. #4Q	1484	nr	51	nr	209	35	12	575
#5–2	20	–	–	nr	8	1	–	80
Stem #5	20	–	–	nr	8	1	–	80
#6–2	337	3	6	3	6	13	19	50
#6–3	10	–	–	–	–	–	–	40
#6–6	58	nr	5	–	–	1	–	130
Stem #6	405	nr	11	3	6	14	19	220
Total	6953	nr	970	nr	1109	229	70	3545

(* Internode #3–1 accidentally destroyed on 1 February, whereupon the ants emigrated with their brood and a few small pseudococcids to other internodes.)

worker populations were standing close together (cf. Fig. 1): #2 with 2461 workers in 10 internodes, #3 with 2363 workers in 14 (originally 15) internodes, and #4, the queenright stem, with 1484 workers in 5 internodes. The remaining 3 stems (#6, #1, #5) had 405, 220, and 20 workers in 3, 2, and 1 internodes, respectively.

Internodes #3–19 and #6–7 were empty, although they had suitable entrance holes and traces of mealybugs formerly attached to the walls indicated a former occupation. The five topmost inhabited internodes of stem #3, #3–20 to –24, contained no or only very little brood; they were rather moist, and only young pseudococcids were present. Internode #3–24 even contained some water which the ants were engaged in carrying outside. We conclude that these chambers had only recently been added as nest sites by the colony.

The nests of the four partially collected colonies (17 internodes from 6 stems), of which one was queenright, contained between 25 and 338 workers. In all, there were 2 nests with over 300 workers, 2 (including the queenright one) with 200–299 workers, 6 with 100–199 workers, and 7 below 100 workers.

3. Size and distribution of alate populations; sex ratios

Among the 2079 alates (adults and pupae combined) of colony BM1, 970 were gynes and 1109, males. Sexuials were numerous in chambers that contained many workers ($r = 0.778$, $p < 0.001$) (Tab. 1, Fig. 2); a positive correlation between alate and worker number was also observed in the 17 internodes of the partially collected colonies ($r = 0.784$, $p < 0.001$). An exception was the queen chamber (#4–1), where – despite the largest worker population of any nest – one male pupa was the only sexual found. Also during the relocation of the likewise populous queen nest of a second colony, BM2, we observed transportation of only two adult males and five male pupae but no gynes to an internode in a neighboring stem. When this internode was collected ca. one month later, 16 adult males but no other sexuials were found in it, along with 281 workers. This indicates that in the queen chamber no female sexuials and only a few males are reared despite the presence of a very large worker population. Presumably newly occupied chambers (#3–20 through –24) also did not contain sexuials except for a few adult males.

The overall numerical sex ratio of BM1 was 0.88:1 (gynes:males). This was approximately also the numerical sex ratio in each of the two queenless stems with the largest ant populations (stem #2: 1.00:1, stem #3: 1.06:1), but in the queenright stem, #4, the sex ratio was 0.24:1, i.e., strongly male biased, probably due to a suppression of gyne development in the close vicinity of the queen. Comparison of census data of another, albeit only partially censused colony reveals a similar difference in sex ratio between a queenright and a queenless stem (two nests from queenright stem: 353 workers, no gyne, 17 males; one nest from queenless stem: 135 workers, 23 gynes, 7 males).

The combined numerical sex ratio of all *Te*-populations that we have collected so far is 0.96:1 (970 gynes and 1109 males from colony BM1 plus 133 gynes and 37 males from the remaining nests).

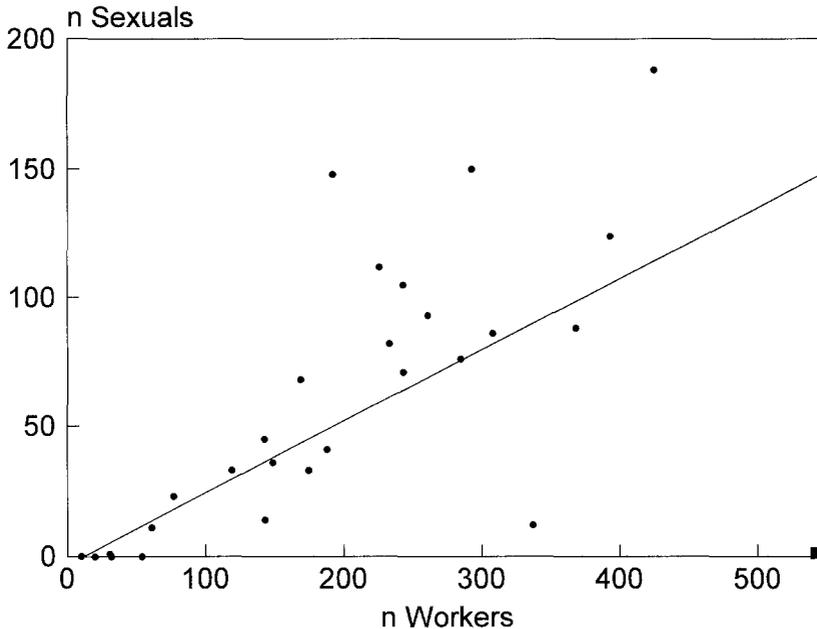


Figure 2. *Tetraponera* sp. PSW-80: Relationship between alate and worker number in the queenless nests of colony BM1. Black quadrat: Queenright nest (for comparison)

For a meaningful sociobiological interpretation, the investment ratio into sexuals, not the numerical sex ratio, is of interest. We determined the dry weight ratio of individual alates, based on the averages of 7 gynes ($6.25 \text{ mg} \pm 1.10 \text{ mg}$) and 7 males ($2.04 \text{ mg} \pm 0.19 \text{ mg}$) as 3.057:1. Multiplied with the numerical sex ratio this results in an estimate of the investment sex ratio of 2.69:1 for colony BM1, or of 2.93:1 for the sum of all *Te*-populations censused so far, a close approximation to the 3:1 ratio predicted for outbred ant populations with monogynous colonies in which the queen produces (virtually) all the males (Trivers and Hare, 1976).

In those internodes of BM1 where adults and pupae were censused separately (representing ca. 75% of all sexuals), 86.6% of the gynes ($n = 774$) but only 48.6% of the male sexuals ($n = 866$) were adults. There is therefore some indication, corroborated also by our laboratory observations on swarming behavior and from Terron's (1970) study on *Tetraponera anthracina* Santschi, that the males leave the nest somewhat earlier than the females. If males do indeed leave the nest earlier than females, the true numerical sex ratio (as determined by counting all alates reared over the whole reproductive season) of *Te* would be more male-biased than the sex ratio determined from the colony composition on the day of collection.

Swarming or searching *Te* queens were seen in February and October (Klein et al., 1992). Alates were found to be present in the colony every time nests were collected, so far in February, March and August. The proportion of sexuals (as percentage of all adults and pupae combined) was similar in March (5.8% in 7 nests, incl. a queenright one; 6.6% in the 6 queenless nests) and August (6.5% in 10 queenless

nesses). In February, 16.0% of all adults in 28 nests were sexuals (based on colony BM 1, Tab. 1, where inclusion of pupae was not possible as worker pupae were not counted), a considerably higher proportion than in March and August. In other Pseudomyrmecinae alates are produced on a year-round basis and mating flights may occur daily in all seasons (Janzen, 1966, 1973; Terron, 1968, 1970; Ward, 1985). So far we have no reason to assume that *Te* should be different.

4. Observations on brood composition and brood tending

Eggs nearly exclusively were found in the queen chamber. Small larvae also predominated there, whereas all the other internodes contained mainly medium-sized and large larvae, prepupae, and pupae (workers and sexuals). A similar difference in brood composition between queenright and queenless chambers was observed during relocation experiments with another colony. During two relocations all brood items carried away by the workers were recorded. The results were:

Queenright chamber: 33 worker pupae, 5 male pupae, 14 prepupae, 339 larvae (mostly small), 186 eggs;

Queenless chamber: 21 worker pupae, 57 larvae (mostly medium-sized and large), 2 eggs.

Inside the internodes the larvae and pupae possibly do not lie on the bottom of the chamber, but instead stick to the walls or are held by workers. Peeking through a gently opened hole in the wall, we saw many workers sitting head down on the walls, each keeping a brood item in the mandibles. We cannot exclude the possibility, however, that this observation is an artefact: the larvae and pupae may normally be attached to the walls, but the workers had picked them up because of the disturbance, as they do quickly when their laboratory nests are disturbed.

In laboratory nests (plastic petri dishes, plastic bowls, and film vials, all with plaster of paris bottom) the brood was usually lying on the ground, perhaps because the walls were too dry and slippery. When laboratory nests were flooded for experimental purposes, the workers attempted, often successfully, to attach the immatures to the walls or ceiling. Some immatures, especially eggs, were at times seen sticking to the ceiling (only eggs) or walls for many successive days.

5. The trophobionts of *Tetraoponera* sp.: *Kermicus wroughtoni pseudococcids* inside the bamboo

All internodes which were occupied by the ants also housed mealybugs of a species, *Kermicus wroughtoni*, described from specimens collected in India, where they were tended by the ant *Oecophylla smaragdina* (Newstead, 1897). We distinguished three size classes: large: ca. 5 mm or more; medium-sized: of variable intermediate length; and small: up to ca. 1.5 mm. Small specimens are carried by swarming young queens (Klein et al., 1992) and by workers during nest relocations (unpubl. obs.). Internodes with few workers contained only small pseudococcid nymphs, whereas those with sizable ant populations usually contained a considerable number of medium-sized

and large pseudococcids in addition to small ones (Tab. 1). Small pseudococcid specimens (ca. 3545) by far outnumbered the medium-sized (70) and large ones (229). Most of the pseudococcids (71.4% of the large ones, 75.0% of the medium-sized ones, and 71.7% of the small ones) were sitting on the ceilings of the internodes (= the undersides of the transverse nodal walls), much fewer on the internode bottoms (= upper sides of the transverse walls), and very few on the peripheral internode walls except for the first ca. 5 cm above and below the nodes.

Similar observations on the numerical relationship between the ants and the pseudococcids and on the location of the pseudococcids within the internodes were made in the four partially collected colonies.

The preference for the upper part of the internode is probably a consequence of the higher moisture in the lower part, where sometimes water accumulates (which the ants then drink and spit out of the nest entrance (Klein et al., 1993)). In some internodes we found a number of circular spots of wax indicating places from which a pseudococcid had been removed. In the queen chamber of BM 1, 18 empty places of large pseudococcids were detected besides 85 small, 2 medium-sized, and 10 large live individuals. Probably this was the oldest inhabited internode, perhaps the queen had founded the colony there. Deserted places may indicate that either (1) the mealybugs had been moved to another place; or (2) had died and been removed; or (3) had been eaten by the ants.

Discussion

The particular nesting habits of *Te* provide a unique chance to study in detail the colony structure of a monogynous polydomous ant species with large colonies. They also allow a look at the causes and effects of plant specialization in ants. The internodes and bamboo stems containing parts of the *Te*-colony are strictly separate from each other. They are only accessible through holes in their external walls which, like the node septa, can not be penetrated by the ants because of their extreme hardness. Distances between entrance holes may amount to several meters in many cases, and the outer or upper internodes may be 8 m or more away from the queen chamber. Nevertheless, the workers evidently carry eggs and/or small larvae from this chamber to the other subunits ("nests") of the colony where workers and sexuals are reared. Judging from the fact that only few eggs, if any, were found in the queenless internodes, egg-laying by workers seems improbable (cf. also Terron, 1970, 1977). Also the overall investment sex ratio of 2.93:1 (biomass gynes:biomass males) corresponds closely to the 3:1 ratio predicted for monogynous species of eusocial Hymenoptera in which the queen produces all males (Trivers and Hare, 1976). Because adult females probably remain inside the nest longer than adult males, however, the true investment sex ratio may be more male-biased than our data indicate.

Except for very sporadically occurring bursts of heavy outside activity, *Te* workers are rarely seen foraging. On one occasion we saw a dozen or so workers exploiting some bird droppings about 5 m from the nest and in another case a part of

a reduviid bug was carried toward an entrance hole by several workers; D. Kovac (pers. comm.) witnessed the harvesting of a dry mushroom on the ground several meters from an inhabited culm over the course of several days. Insect pieces offered to the ants were often not accepted, but sometimes there was instantaneous heavy recruitment upon the discovery of fresh insect meat. Starved laboratory colonies recruit very efficiently to both honey water and insect meat (Klein, 1990). Probably most of the food requirements of the colony are met by its symbiotic pseudococoids in the form of honeydew. Possibly, some of the mealybugs are consumed, as suggested by the observation of "empty places" inside the nests, with traces of pseudococoids formerly sitting there. However, we did not find any recognizable pseudococcid parts (e.g., the long stylets) in 10 larval food pellets that we investigated. 6 pellets contained largely unidentifiable insect parts (including what looked like remains of a small ant and of a small unidentified Hymenopteran), 2 of these, also ?fungal hyphae, a 7th pellet included thick walled hexagonal ?plant cells, and the remaining pellets, unidentifiable matter. *Te*-workers, queens, and males possess a highly unusual structure in their digestive system; a midgut/hindgut protrusion (length ca. two times the gut diameter) embedded in a dense ball of tracheae and Malpighian tubules. The Malpighian tubules (16–18) arise from the crown of the protrusion. Four other Pseudomyrmecinae checked for comparison, *Tetraponera modesta* (F. Smith), *T. pilosa* (F. Smith), *Pseudomyrmex mexicanus* (Roger), and *P. pallidus* (F. Smith), lack this structure. Possibly this midgut/hindgut pouch is an adaptive feature allowing the digestion of certain types of plant food, maybe a symbiont chamber.

A monogynous polydomous colony structure is not exceptional among ants (Snyder and Herbers, 1991), but often only 2 or 3 nests are occupied by one colony (Hasegawa, 1992; Snyder and Herbers, 1991), and polydomy may vary with season. Our main study colony inhabited 36 nests, of which only one was queenright, and another colony probably occupied far more than the 29 internodes we found to be inhabited during our observations from the ground. The colony structure of *Te* thus comes close to that of the huge monogynous but highly polydomous weaver ant colonies of the genus *Oecophylla* (Way, 1954) or other polydomous arboreal ants with large colonies, including plant-mutualistic Pseudomyrmecinae (Janzen, 1967; Schremmer, 1984). As in *Myrmica* (Snyder and Herbers, 1991) or in *Pseudomyrmex seminole* (Klein, 1987a), female sexuals are reared only in the queenless nests, not in the chambers containing a queen. The queen evidently suppresses gyne formation in her nest completely and partially in the immediately adjacent internodes (numerical sex ratio 0.24:1 in stem #4, but close to 1.00:1 in other stems; cf. Tab. 1). A queen effect like this is known also from other ants (Brian, 1980).

Polydomy appears to be frequent in the subfamily Pseudomyrmecinae (Janzen, 1966, 1973; Schremmer, 1984; Ward, 1985; Klein, 1987a). Klein (1987a) reports on three polydomous *Pseudomyrmex* species from Florida, two being facultatively polygynous, one always monogynous. These species and several congeners of nearctic distribution (Ward, 1985) usually inhabit dead branches in trees and shrubs. Like generalized *Tetraponera* species from Malaysia (see introduction) and Africa (Terron, 1970) they forage for insect prey and honeydew on leaves and twigs or visit extrafloral nectaries. Apparently most species have small colonies of no more than a few hundred adults (Janzen, 1966; Terron, 1968; Ward, 1985; Klein, 1987a; unpubl.

obs. in Malaysia). As in *Te*, “queenless nests account for the bulk of alate production” (Klein, 1987a) in the polydomous *Pseudomyrmex* species from Florida.

The monogynous, polydomous colony structure of *Te* thus is quite well in accord with that of other Pseudomyrmecinae. The large colony size, however, is comparable only to that of the plant-mutualists within the subfamily (e.g., Janzen, 1967, 1972; Schremmer, 1984). Also the ovaries of *Te* show an adaptation for large colony size. Whereas generalized Pseudomyrmecinae tend to have 2 ovarioles per ovary (e.g., *T. anthracina* (Terron, 1970), *T. modesta*, *Pseudomyrmex mexicanus*, *P. pallidus* (unpubl. obs.), *Te*-queens have 10 ovarioles per ovary. Unlike the plant mutualistic Pseudomyrmecinae, *Te* workers are not at all aggressive toward other insects or larger animals and do not seem to provide any protection to their host plant. Instead, *Te* relies on the physical features of its host plant for its own protection: the strong walls of the bamboo culms combined with very narrow entrance holes that can be blocked easily by one to a few ants. But *Te* has evolved an elaborate system of pseudococcid-tending inside the bamboo stems, comparable to that of many pseudomyrmecine plant mutualists (Janzen, 1972; Schremmer, 1984; Ward, 1991), by which it secures itself a rich, well protected nutritional basis within its nests. Moreover, the queens carry young pseudococcid nymphs with them on the nuptial flight (Klein et al., 1992), allowing them a quasi-claustral mode of colony foundation; and the workers remove water that may collect (for example during heavy rainfall) in their internodes (Klein et al., 1993), thereby extending the average time of possible nest occupancy. The exceptionally large – for a non-mutualistic pseudomyrmecine – colony size of *Te* is certainly the consequence of its efficient exploitation of bamboo internodes as both a rich competition-free food source (via the symbiotic Pseudococcidae) and well protected nesting space.

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