

Research article

## *Polyrhachis loweryi* (Formicinae): A guest ant parasitizing *Rhytidoponera* sp. (Ponerinae) in Queensland, Australia

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**Summary.** At the type locality near Miles in Queensland, Australia a queenright colony of *Polyrhachis loweryi* was found (1 dealate queen, 91 workers, males and brood) within a colony of *Rhytidoponera* sp. (near *aciculata*), whereas other colonies of this *Rhytidoponera* species contained only a few workers of *P. loweryi*. For experiments and behavioural observations *P. loweryi* and its hosts were kept in the laboratory for some time. The queenright *P. loweryi* colony constructed closed nests out of soil and plant fibres, within the host nest, and only containing *Polyrhachis* specimens. *P. loweryi* workers in part, remained amid the assembly of *Rhytidoponera*, from whom they obtained carbohydrate and protein food. In addition, *Polyrhachis* workers regularly left the host nest. They were able to collect liquid carbohydrate food and to distribute it among conspecific nest mates via trophallaxis. The care of the *P. loweryi* brood was fully done by *P. loweryi* itself. However, *Rhytidoponera* workers were observed carrying *P. loweryi* brood in addition to their own brood. In artificially induced nest relocations, *P. loweryi* was able to move to a new nest independently from its host ants, displaying the typical invitation behaviour, trail laying behaviour, and leader independent trail communication found in other members of the genus. *Rhytidoponera* sp., which in addition to inconspicuous trail marking, performs nest relocation via social carrying, rarely but regularly also carried *P. loweryi* to the new nest. Whereas *Rhytidoponera* sp. workers were carried in the typical ponerine posture, *P. loweryi* workers were carried by them in the formicine posture. We conclude that *P. loweryi* is best described as a guest ant of *Rhytidoponera* sp.. The species seems to be less well integrated into the societies of its *Rhytidoponera* sp. host than the closely related *P. lama*, a social parasite of *Diacamma* sp. in Java.

In both *Polyrhachis* species workers from queenright colonies perhaps emigrate with a few eggs or larvae in order

to rear them in neighbouring host nests. The adaptive and predispositional reasons for the phyletic development of this parasitic relation remain unclear.

**Key words:** *Diacamma* sp., Formicidae, *Polyrhachis loweryi*, *Rhytidoponera* sp., social parasitism

### Introduction

Social parasites are not uncommon in most major groups of social insects. In ants, they have evolved in comparatively high numbers and in a unique sociobiological diversity. Most parasitic ants, i.e.inquilines, slave-makers and temporary parasites, are closely related to their respective host species, a fact which was termed “Emerys rule” (Le Masne, 1956). Xenobiotic or guest ants, on the other hand, coexist with host species belonging to different tribes or even subfamilies. The recent discovery of a formicine parasite, *Polyrhachis lama* Kohout, 1994, living nearly like an inquiline within the nests of a ponerine, *Diacamma* sp. in SE-Asia (Maschwitz et al., 2000), seemed to indicate an evolutionary pathway to a permanent, true social parasitism in which a close systematic relationship was not a necessary predisposition, a parasitism not obeying “Emery’s rule”. The highly sophisticated parasitic relation suggested a long phyletic development. *P. lama* belongs to the *viehmeyeri* species-group of the subgenus *Myrmhopla* Forel, 1915 (Kohout, 1994b). The range of *P. lama* apparently extends from Java and Hong Kong to the Himalayas (Maschwitz et al., 2000; Kohout, 1994a and unpublished data). Further nine species of this group are restricted to Australia and neighbouring islands, i.e. New Guinea, Aru Islands, Solomon Islands and Seram (Kohout, 1990). Collecting data of three Australian species, *P. eremi-*

ta Kohout, 1990, *P. rustica* Kohout, 1990 and *P. loweryi* Kohout, 1990 indicated that they perhaps also were associated with ponerine ants, though with species of the genus *Rhytidoponera* (Kohout, 1990, 1994b). In February and March 2000 we searched for these 3 species at their former collection sites. One of them, *P. loweryi*, was found, associated with a *Rhytidoponera* species. This record and the preliminary results of behavioural studies are presented here.

## Material and methods

### Field collecting

We visited the type localities of *Polyrhachis rustica* (at Mareeba, 17°01'S, 145°24'E and near Collinsville, 20°31'S, 147°49'E), of *Polyrhachis eremita* (near Marlborough, 22°43'S, 149°45'E) and of *Polyrhachis loweryi* (near Miles, 26°36'S, 150°10'E) (see Appendix). Since all three species originally had been found in more or less close association with large *Rhytidoponera* species, we searched for nests of such species which then were excavated as completely as possible. Nests of smaller *Rhytidoponera* species (belonging to the *metallica* species-group) also were checked for the presence of *Polyrhachis* specimens. Nests were dug out and the nest material thrown onto a large plastic sheet. The ants were sorted from the soil, transferred into a plastic vessel, and then carefully checked for the presence of a different species. At Mareeba (21 colonies of a large brownish *Rhytidoponera* sp. checked), and at Collinsville (15 colonies of a large black and one of a large brownish-black *Rhytidoponera* sp. checked) we did not find any *Polyrhachis rustica*. At the site of *P. eremita*, near Marlborough, no nests of any large *Rhytidoponera* sp. were found, probably due to serious deforestation. At Miles, a total of 10 colonies of a large *Rhytidoponera* sp. (belonging to the *aciculata* species-group, H. Reichel, pers. comm.) were dug out in a dry sclerophyll forest. Six of these colonies contained specimens of *Polyrhachis loweryi* (Table 1), including one queenright mixed colony. They were transferred to the laboratory for behavioural studies. In five colonies of another, black *Rhytidoponera* sp. (belonging to the *convexa* species group, H. Reichel pers. comm.) no *Polyrhachis* were detected. Voucher specimens have been deposited in the Queensland Museum, Brisbane, Australia and the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

### Dissection of ants

Dissections of the *Polyrhachis loweryi* specimens were made to check their reproductive status as described by Buschinger and Alloway (1978) under a dissecting microscope. No efforts were made to identify egg-laying specimens of the *Rhytidoponera* sp. whose queens are morphologically indistinguishable from the workers.

### Laboratory culture of *Polyrhachis loweryi* and *Rhytidoponera* sp.

The large queenright mixed colony of *P. loweryi* which had the original colony composition was kept in a wooden arena (50 × 150 × 10 cm), with a plastic box (20 × 20 × 10 cm) inside, as a nest chamber. The nesting ground was covered with plaster of Paris and cardboard (egg-containers) was offered as a nest shelter. The smaller colonies were held in arenas (60 × 30 × 10 cm), also provided with nest chambers of the same size as above. Inside the arena, water, honey water and protein food (cut cockroaches and *Tenebrio* larvae) were provided *ad libitum* in small dishes. Further experimental details are reported in the results section.

## Results

### Characterization of the host ant *Rhytidoponera* sp. (*nr. aciculata*)

*P. loweryi* was discovered in colonies of a large *Rhytidoponera* species at the type locality, 5 km from Miles in a relatively little disturbed sclerophyll forest. The *Rhytidoponera* workers were 1.2–1.3 cm in length and blackish-brown in colour, with the gaster slightly lighter. The colonies were easily recognized, because they had entrance hills of up to 9.5 cm height and 36 cm diameter. The nests could be more than 65 cm deep (where we had to stop excavation because of extremely hard soil). They consisted of a more or less vertical entrance tube, widening up to three superimposed floors of large flat chambers, up to 30 cm wide, of irregular shape and partly ending in short distal tunnels. As the workers quickly fled into deeper chambers, their actual distribution in the nest remained unknown. Most ponerine colonies had no brood. In one colony pupae and a few small *Rhytidoponera* larvae were found. A plethora of “guests” inhabited the

**Table 1.** Census data of *Rhytidoponera* sp. (*nr. aciculata*) colonies with and without the parasitic *Polyrhachis loweryi*

| Col. # | number of <i>Rhytidoponera</i> sp. |        |       | number of <i>Polyrhachis loweryi</i> |        |       |               |                     |
|--------|------------------------------------|--------|-------|--------------------------------------|--------|-------|---------------|---------------------|
|        | adults                             | larvae | pupae | workers                              | queens | males | adult females | eggs, larvae, pupae |
| 1      | 41                                 | –      | –     | 6                                    | –      | –     | –             | –                   |
| 2      | 108                                | –      | –     | 7                                    | –      | –     | –             | –                   |
| 3      | 167                                | –      | –     | 5                                    | –      | –     | –             | –                   |
| 4      | 46                                 | –      | –     | –                                    | –      | –     | –             | –                   |
| 5      | 238                                | –      | –     | >91                                  | 1      | +     | –             | +                   |
| 6      | 132                                | –      | –     | 6                                    | –      | –     | –             | –                   |
| 7      | >240                               | –      | –     | –                                    | –      | –     | –             | –                   |
| 8      | ≥400                               | –      | +     | –                                    | –      | –     | –             | –                   |
| 9      | >251                               | +      | +     | >19                                  | –      | –     | –             | –                   |
| 10     | >100                               | –      | –     | –                                    | –      | –     | –             | –                   |

*Rhytidoponera* nests. Great numbers of larvae and adults of a cockroach species, many woodlice (*Nagaroides tumidus* (Trachelipodidae); det. F. Taiti, Firenze), a few specimens of a small reddish spider and a number of crickets and lepidopterids crowded all nest chambers and tunnels of *Rhytidoponera* nests with and without *Polyrhachis*.

#### Characterization of *Polyrhachis loweryi*

The *P. loweryi* workers were 0.7 to 0.8 cm in length and black, thus distinctly differing in size and colour from their hosts. They were found in 6 out of 10 *Rhytidoponera* sp. (nr. *aciculata*) colonies (Table 1). Three of the large colonies without *P. loweryi* were dug out only in part (# 4, 7, 10 cf. Table 1) so that we cannot exclude that single *P. loweryi* workers were also present in these nests. Similarly, only a minor part of colony # 9 was excavated so the ants were not censused completely. Two types of *P. loweryi*-infested colonies could be distinguished. Type 1 colonies (# 1, 2, 3, 6) each had less than 10 *P. loweryi* workers. Type 2 was represented by one big colony (# 5) with a *P. loweryi* queen, numerous workers (> 90) and a few black males. Since the small part of colony # 9 that could be dug out, contained almost 20 *P. loweryi* workers, this colony probably can be attributed to type 2, and we suppose that it was also queenright. In the large colony # 5, workers and males of *P. loweryi* were already found in the upper nest region. At the level of the first horizontal chamber we came upon an almost pure group of *P. loweryi* indicating that they were separated from their hosts at least in part. In the deeper galleries parasite and host ants were fully intermingled, probably because they were disturbed by our digging. In addition to the brown *Rhytidoponera* sp., five colonies of a black *Rhytidoponera* species (belonging to the *convexa* species group) of similar size were found at the collecting site. We did not discover any *Polyrhachis* specimens when checking these colonies.

#### Reproductive status of *P. loweryi* workers

The ovaries of six *P. loweryi* workers were dissected immediately after collection to check their reproductive status, two from colony # 1, two from colony # 6 (both queenless), and two from the queenright colony # 5. Each ovary consisted of two ovarioles, thus each worker had a total of four. None contained any developing yolky eggs, nor were corpora lutea detected. After four months in the laboratory, all 11 remaining *P. loweryi* workers of colony # 9 were dissected. This queenless worker group had regularly produced a few eggs and larvae during this time but raised up no pupae and adults. The brood had obviously been produced by one worker that possessed an unusually high number of 2 × 5 ovarioles and corpora lutea, though at the time of dissection, we found no large eggs in the ovaries. The eggs were small to medium sized and similar to those of the remaining ten workers, which had no corpora lutea. Morphologically the reproductive specimen was an ordinary worker. The ovariole numbers in the 11 workers were 10, 5, 4, 4, 4, 4, 3, 3, 3, 2.

#### Demographic development of the queenright colony # 5 after excavation

In the large queenright *P. loweryi* colony egg laying soon commenced as well as larval development, pupation and worker eclosion. We observed that always workers hatched from the light brownish pupae. In the first 50 days of observation, the queenright colony (which then contained 52 workers) produced 12 young workers. Several *Rhytidoponera* sp. colonies, including colony # 6, also produced brood in the first months of laboratory rearing (April–September) with young workers hatching from blackish-brown pupae. Later on *Rhytidoponera* sp. brood production stopped in all nests, though the colonies were amply fed with various protein sources and with honey water. After 5 months, brood production began again indicating a cyclic brood production process in this species.

#### Intraspecific behaviour of *Rhytidoponera* sp. (nr. *aciculata*)

##### Food collection and brood care behaviour

Protein food, i.e. insect pieces, were collected by *Rhytidoponera* sp. workers, carried into the nest and offered to the *Rhytidoponera* larvae. Carbohydrates, i.e. honey water, was imbibed by the *Rhytidoponera* workers. Droplets taken between the mandibles were offered both to conspecific and *P. loweryi* workers. Laboratory observation showed that *Rhytidoponera* brood was exclusively cared for by their own workers at sites separate from the *Polyrhachis* brood.

#### Intraspecific behaviour of *Polyrhachis loweryi*

##### Nest building behaviour

During several months of observation it became obvious that *P. loweryi* workers built a separate nest chamber within the *Rhytidoponera* nest. With shredded cardboard, taken from the artificial *Rhytidoponera* nest chambers, and with paper fibres, they walled off a space with a square area of about 4 × 8 cm and a volume of almost 50 cm<sup>3</sup>. The carton wall had one or two roundish openings of 0.5 cm in diameter, narrow enough to exclude the bigger *Rhytidoponera* workers. In 8 experiments, where we destroyed these chamber walls, *P. loweryi* workers repaired them or built a new chamber within a few days. Apparently larval silk (used by other *Polyrhachis* species belonging to the subgenus *Myrmhopla*) was not used for carton formation in *P. loweryi*.

##### Extranidal stay and food collection of workers

During four months of observation every 2–3 days we regularly observed single *P. loweryi* workers within the arena. The mean ratio of *Rhytidoponera*/*Polyrhachis* workers, counted at several times during laboratory maintenance outside the nest, was 5 : 1. In contrast the determined mean ratio of workers in the nest was 2.5 : 1. *P. loweryi* workers thus left the nest

less frequently than *Rhytidoponera* workers. *P. loweryi* workers never collected protein food, i.e. insect pieces, but occasionally drank honey water directly from the offered source. After this they returned to the nest and offered the fluid to other *P. loweryi* workers with opened mandibles. These trophallactic worker contacts occurred 3–9 times ( $n = 15$ ), within 45 minutes after initial food application. Each trophallactic exchange took up to two minutes. Most of the honey water collectors did not return to the feeding site for taking up liquid food during the next one hour. Recruitment of further carbohydrate collectors was never observed. After an experimental reduction of the colony size of the host ant of about 50%, the food collecting behaviour of *P. loweryi* changed in an obvious way: up to five *P. loweryi* workers simultaneously collected carbohydrate liquid food in the arena. We did not observe *P. loweryi* workers carrying any visible insect parts. Several times, however they imbibed haemolymph which they carried into the nest.

#### *Behaviour of P. loweryi in isolation*

The whole *P. loweryi* colony was isolated to check its demographic development and the ability to forage for food on its own. Therefore *P. loweryi* was brought into a large separate arena, with a small Petri dish as a nest, proteins and carbohydrates were offered in the arena. We observed the colony during one month for 45 minutes each day. We recorded between 1–59 protein contacts by the workers in the 45 minute periods, but they never carried any protein food particles into the nest. Most contacts lasted for one second. Rarely, i.e. in seven instances the workers stayed for longer, up to 56 seconds, and we observed protein licking, sometimes with several interruptions. Contact with liquid carbohydrate food occurred between one and 21 times during the observation periods, with a duration of up to several minutes. Liquid carbohydrate food and sometimes also protein fluid were brought into the nest, and distributed among nest mates. However, after one month of observation, we noticed that all eggs had disappeared. Large larvae did not develop into pupae during this time but stopped growing. Worker number also decreased from 126 to 95. After this experiment, we reconnected the *P. loweryi* colony with the *Rhytidoponera* sp. colony via a bridge. When checked after three days the *Polyrhachis* had found their hosts, and had completely moved back into their nest. After one month without disturbance, we found new *Polyrhachis loweryi* eggs, larvae and pupae.

#### *Brood care behaviour*

*P. loweryi* brood exclusively was found within *P. loweryi* assemblies, and often was held in the mandibles of the workers. When *Polyrhachis* brood, taken from a different *Rhytidoponera/Polyrhachis* colony, was artificially offered to *Polyrhachis* workers, they immediately took up the eggs, larvae and pupae and carried them to the other *P. loweryi* brood within the nest. The *P. loweryi* workers cared only for brood

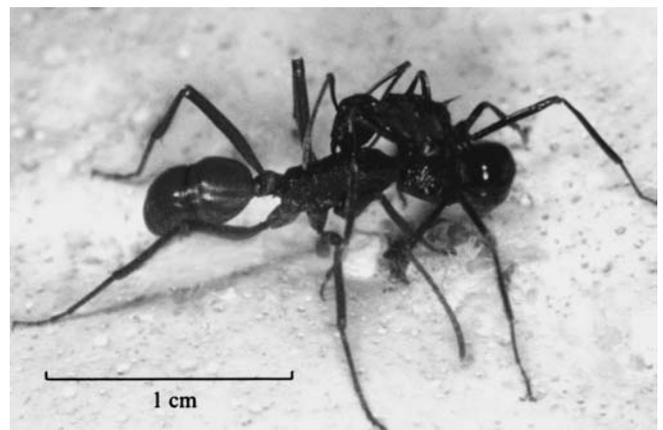
of their own species. We did not investigate in detail how they fed their larvae, but from our behavioural observations it was obvious that the larvae were fed by regurgitated food. *P. loweryi* did not contact the ponerine brood at all.

#### *Interactions between host and parasite*

During excavation of the queenright colony in the field only very few *P. loweryi* larvae were discovered. We observed that *P. loweryi* workers and males concentrated in certain areas of the nest, however, workers and males were also found in other nest parts. Thus we imitated the three-dimensional structure of the natural nest in the laboratory by offering two layers of egg-container carton, and checked the residence site of *Polyrhachis* workers, queen and brood. *P. loweryi* always congregated at one point of the nest interior, a small distance (3–7 cm) from the main assembly of *Rhytidoponera*. However, a few workers were always found within the *Rhytidoponera* assembly.

#### *Behavioural interactions between workers of P. loweryi and Rhytidoponera sp.*

*P. loweryi* frequently displayed a peculiar behaviour towards its *Rhytidoponera* host, both within and outside the nest. Upon contact, the guest workers frequently intensively antennated the host ants, most frequently in the head area but also on the alitrunk and gaster, and pushed them slightly with their mandibles and licked them. After this they frequently climbed partly or even fully onto the head and alitrunk of the host ants, while licking and antennating them continuously (Fig. 1). Other *P. loweryi* workers were also treated in the same way. During this behaviour *P. loweryi* workers preferentially came in contact with host ants which transported honey water into the nest. After displaying typical begging behaviour towards the *Rhytidoponera* worker (antennating the mouth region), *P. loweryi* very quickly imbibed the liquid, subsequently offering it to other *P. loweryi* workers.



**Figure 1.** Mounting behaviour of *P. loweryi* and its host *Rhytidoponera* sp.

### Behaviour of *Rhytidoponera* sp. toward *P. loweryi* brood

*Rhytidoponera* sp. carried all kinds of brood when they were experimentally offered within the arena as well as in the nest interior. While they readily and immediately took their own brood, *P. loweryi* brood was taken reluctantly. Three to six contacts were necessary until a *Rhytidoponera* sp. worker took up the guest brood, i.e. eggs, larvae or pupae, carried it into the nest and deposited it on a brood batch ( $n = 20$ ). When *Rhytidoponera* sp. carried brood of *P. loweryi*, the *P. loweryi* workers soon discovered this brood, contacted the host ants with severe antenna movements and as a rule, immediately took over their brood. No signs of aggressiveness were observed during this behaviour.

### Experimental intra- and interspecific worker exchange

Workers of *Rhytidoponera* sp. brought into alien colonies were soon severely attacked by their conspecifics. However, in several experiments, when whole *Rhytidoponera* colonies of about equal size were mixed, no aggression occurred. Workers of *P. loweryi* brought into non-parasitized, alien *Rhytidoponera* sp. colonies, mostly did not release any aggression by the alien host ants. Upon contact with the host workers they showed the typical antennating, licking and mounting behaviour. In 4 of 22 cases, they were slightly attacked initially, but after intensive antennating and a ventral bending of the gaster toward the host ant, the *Rhytidoponera* workers were “soothed” and *P. loweryi* was soon accepted. Only in 2 of 22 cases, *P. loweryi* workers were seriously attacked. We stopped the experiment in these cases. When we brought alien *P. loweryi* workers into a mixed colony (*Rhytidoponera* sp./*P. loweryi*) we did not observe any aggressive behaviour from the host ants in all of 25 cases. Comparing the interspecific behaviour between host ants from non-parasitized and from mixed colonies, we observed a more aggressive behaviour by non-parasitized host ants towards *P. loweryi* workers, which were evicted from the nest and brought into the arena. However, a total of 44 of 47 *P. loweryi* workers were eventually accepted in parasitized and pure *Rhytidoponera* colonies combined (Fishers Exact Test,  $p < 0,01$ ). When a *P. loweryi* worker met an alien conspecific in the arena, it usually did not release any aggressive behaviour. In only 1 out of 15 cases, the alien worker was attacked and stretched by its legs and antennae by two *P. loweryi* workers. In all other instances the discovered “intruder” was treated in an excited but non-aggressive way. First the intruder was intensively antennated from both sides, then its whole body was licked and lastly trophallaxis occurred. In 14 cases the intruder was carried into the nest by a *P. loweryi* worker.

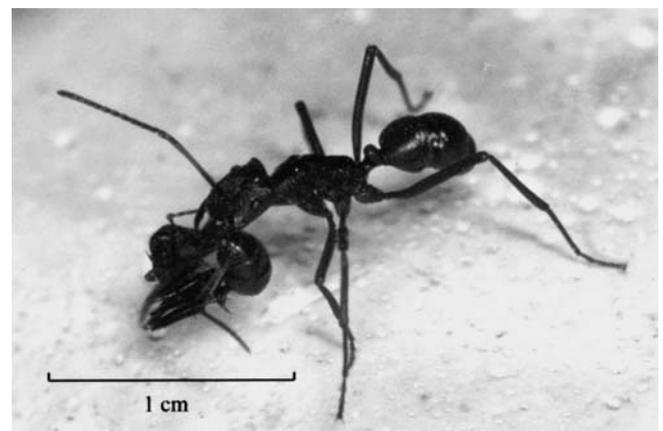
### Colony relocation

Colony relocation behaviour of the whole mixed queenright colony # 5 or parts of it were released both in *Rhytidoponera*

sp. as well as in *P. loweryi* by moving the ants into a large arena. A plastic nesting box was then offered a) directly on the arena floor, b) via a flat wooden bridge and c) elevated, via a steep wooden bridge in subsequent experiments. Altogether we performed five colony relocation experiments with the whole large mixed colony (# 5), and another four relocations with parts of this colony.

While *Rhytidoponera* readily accepted the nesting boxes of type a) and b), type c) was not accepted. Colony relocations in experiments of type a) and b) were normally finished after 10–15 hours. *P. loweryi*, on the contrary, accepted all three nesting sites and moved into them within 1–7 hours. During colony relocation *Rhytidoponera* workers performed social carrying and mechanical recruitment behaviour, e.g. slight mandible pulling and jerking movements. Obviously trail laying was not observed, however, according to Hölldobler (pers. comm.) trail laying with gastral gland secretions is known in this ponerine genus.

In contrast to their host ants, successful scouts of *P. loweryi* obviously showed a distinct trail marking behaviour similar to that of other *Polyrhachis* species. In a *Polyrhachis* worker group a motor recruitment display of the scout was observed consisting of jerking head and body movements. Additionally worker transport was observed, where a worker was invited to be carried by jerking movements and slight mandible pulling at the legs or the mandibles. At this *Polyrhachis* workers held each other by their mandibles and showed the typical formicine transport position (Fig. 2). *Rhytidoponera* workers were sometimes invited by *P. loweryi* scouts, however, they immediately recognized their mistake and stopped. Interspecific transport, however, occurred regularly between *Rhytidoponera* scouts and *P. loweryi* workers. In up to 58% of all transport acts during the five colony relocations, the host ant carried *P. loweryi* workers. Interestingly, *P. loweryi* transportees, displayed their specific formicine transport position, indicating that this position is actively performed by the transported worker (Fig. 2).



**Figure 2.** Social carrying of *P. loweryi* by *Rhytidoponera* sp. during colony relocation. At this *P. loweryi* displays the typical formicine transport posture

## Discussion

Before this study, only five workers of *Polyrhachis loweryi* had been collected “in galleries of common large species of *Rhytidoponera*” (Lowery cited in Kohout, 1990). Similarly, the other two Australian species, *P. eremita* and *P. rustica*, were described from 9 and 2 specimens, respectively, which had been collected “together” with unidentified species of *Rhytidoponera*. Thus *P. loweryi* is the first Australian species of the *viehmeyeri*-group for which the regular, and probably obligatory, association with a *Rhytidoponera* species has been confirmed and characterized. Our results indicate that its life history closely resembles that of *Polyrhachis lama* from Java (Maschwitz et al., 2000), the only other *viehmeyeri*-group species whose life history has been investigated in detail (Table 2). These two studies suggest that perhaps other members of the *viehmeyeri*-group may also coexist as social parasites or xenobionts with host ants belonging to the subfamily Ponerinae. Most species in the subgenus *Myrmhopla* apparently have independent life habits (Liefke et al., 1998). The life history of *P. lama* has been described as a kind of inquilinism (Maschwitz et al., 2000), though its relation to the *Diacamma* host is not as intimate as in “true” inquilines where host and parasite obey Emery’s rule, i.e. are very close relatives. *Polyrhachis lama* lives within the nests of its common *Diacamma* sp. host. Though a high number of 48 mixed colonies were checked, only seven contained a dealate *Polyrhachis lama* queen each (two were virgin, though egg-laying). Only *P. lama* workers were found in the other nests. Similarly a *P. loweryi* queen was found in only one out of six mixed colonies although the presence of a queen in a second nest was suspected. The other nests contained only a few *P. loweryi* workers. Workers of *P. loweryi* are apparently less fertile than those of *P. lama*, having undeveloped ovaries.

Originally, parthenogenetic, amphitokous reproduction by *P. lama* workers was suggested (Maschwitz et al., 2000), but subsequent rearing experiments (unpublished) revealed that only males were produced by these workers. In this study no brood was found in mixed colonies containing only *P. loweryi* workers. In addition, in the laboratory only the queenright colony produced new workers. In contrast, in our field surveys in Java, both male and female pupae were found in mixed *Diacamma/P. lama* nests, lacking a *P. lama* queen.

### *Species and colony discrimination*

Occasional light attacks by the host ants demonstrated that odour camouflage of *P. loweryi* may be less perfect than in *P. lama*. The low aggressiveness of both ponerine hosts (*Diacamma* sp. as well as *Rhytidoponera* sp.) toward their *Polyrhachis* guests, or their inability to recognize them as foreign intruders, seems to be the most important prerequisite for the eventual formation of their xenobiotic associations. Whether this is a matter of chemical camouflage of the guest ants, or whether the host species in general are unusually tolerant toward alien Formicinae, remains an open question. However, the extremely high number and diversity of guests (cockroaches, crickets, woodlice etc.) inhabiting the nests of both *Diacamma* sp. and *Rhytidoponera* sp., suggests a comparatively low power of discrimination toward “nest mates”, alien conspecifics and other ant species in these two genera.

### *Communication during nest relocation*

The highly complex subterranean architecture of the large *Rhytidoponera* sp. nests and the distinct character of the nest

**Table 2.** Behavioural similarities and differences between *Polyrhachis loweryi* and *Polyrhachis lama*

|  | <i>P. loweryi</i>   | Similarities  | <i>P. lama</i>  |
|--|---|---|---|
| Nutrition and brood care                     | Frequently forage outside the nest to collect honey water, never collect insect pieces  | Interspecific brood transport by the host during colony relocation or during nest disturbance   | Could be seen rather seldom outside the nest  |
| Nest construction                            | Building its own nest chamber within the host nest, excluding the host  |   | Fully integrated within the host, no nest building  |
| Species and colony discrimination            | Occasional light attacks by the host towards <i>P. loweryi</i>  |   | No attacks occurred   |
| Communication during nest relocation         | Interspecific social carrying; able to perform nest relocation independently from the host; performs mechanical invitation, trail laying, leader independent trail communication, social carrying |   | Fully dependent on the host during nest relocation; performs tandem running with the host |
| Castes and reproduction                      |   | ordinary reproductive system, with mated gynomorphs producing the female brood and workers having male progeny  |   |
| Occurrence of colonies and their composition |   | Until now, both ants exclusively were found in colonies of the host species; queenright colonies are quite rare, most of the mixed colonies comprise only <i>Polyrhachis</i> workers producing male offspring |   |

entrance hills, indicate that this ant, unlike *Diacamma* sp., rarely changes its nest. During artificial nest relocation, social carrying played a dominant role and chemical communication was not obvious. *P. loweryi* was rarely but regularly carried to the new host nest by its host. However the parasite alone was still able to perform its own complete nest relocation, as is known from free living species of *Polyrhachis* of the subgenus *Myrmhopla* (Liefke et al., 2001). Like its nest building behaviour this can also be interpreted as primitive, plesiomorphic trait of its ancestors, not reduced during the evolution of parasitism. Nest relocation is performed in a highly steady and continuous way, an indication of a well developed orientation system. Thus this orientation system might be of relevance in the social biology of this species. In contrast, *P. lama* has fully lost the ability to move nest, though it lays trails outside of the host nest (Maschwitz et al., 2000) to targets, e.g. new or old nesting sites, searching for left brood there.

### *Castes and reproduction*

Former investigations and observations seemed to indicate parthenogenic, amphitokous production of alate gynomorphs, workers and males, by *P. lama* workers (Maschwitz et al., 2000). This hypothesis had been derived from observations during colony censuses in the field, where many queenless colonies (i.e. lacking a dealate queen) contained both male and female (worker and/or gynomorph) pupae, and from dissections of workers that had developed ovaries with yolky oocytes and corpora lutea. However, in extensive laboratory experiments, offspring reared by *P. lama* workers were exclusively male. Manipulated colonies in the field also reared only males (unpublished results). *P. loweryi* apparently has an ordinary reproductive system, too, with mated gynomorphs producing the female brood and workers having male progeny, if any at all.

### *Hypothesis of decentralized brood rearing in P. loweryi and P. lama*

Because of these results and observations, we now suggest that *P. lama* workers carry young brood from the few queenright nests to neighbouring *Diacamma* nests where they rear the larvae using the food supplied by their hosts. We suspect a similar system in *P. loweryi/Rhytidoponera* sp., and that the few *P. loweryi* workers found in *Rhytidoponera* colonies without *P. loweryi* queens had remained there after having reared the brood from their mother colony. At the time of our collecting practically no *Rhytidoponera* broods were present in the nests, perhaps due to a seasonal break in brood production. Also in the 5 colonies of *P. loweryi* without queens, no brood was found. We do not know whether the *P. loweryi* workers return to their old host nest and pick up brood for rearing it in the new host nests. Though highly speculative, this hypothesis is the most probable explanation for our observations in *P. lama* and in *P. loweryi*. The low discrimi-

native power of the hosts (or good chemical camouflage of the parasites) permits the parasite workers to enter neighbouring nests of the host species. The food supplies of the neighbouring host colonies enables them to rear the brood they carry with them, and perhaps such workers may repeatedly return to the queenright mother colony in order to pick up more brood. The trail laying behaviour observed in our nest relocation experiments indicates a well developed orientation ability outside the host nest. The very low aggressiveness of both *Diacamma* and *Rhytidoponera* towards the *Polyrhachis* guests, as shown in this study and in Maschwitz et al. (2000), may facilitate this unique way of “delegating” food supply and brood care to several neighbouring host species colonies. In fact, such behaviour would resemble polydomy in monogynous, independent ants. In addition, the brood in the neighbouring host nests escapes the queen’s influence (reducing gyne formation in favour of worker production), and higher numbers of young gynes can be reared than in the queenright mother colony.

### *The evolutionary origin of the parasitic mode of life in the Polyrhachis viehmeyeri species group*

In our study of the parasitic *P. lama* (Maschwitz et al., 2000) we had supposed that its evolutionary origin must be different from that of typical social parasites obeying “Emery’s rule”. Because of their direct common ancestry with the host species, communication signals and physiological properties of hosts and typical social parasites are similar or equal. As *Polyrhachis lama* and *Diacamma* sp. are not directly related, such evolutionary predispositions are lacking. Because in this instance host and parasite are highly similar in their habitus, a kind of plesiotropic and mimetic relation had been considered as the evolutionary basis of their host-parasite system. In contrast, *P. loweryi* and its *Rhytidoponera* sp. host are much less similar in their habitus, *P. loweryi* being much smaller and of different shape and colour. Mimicry therefore is probably not involved. Since *P. loweryi* has maintained separate nest building within the host nest as well as its own recruitment communication, its parasitic relations most closely resemble those of traditional guest ants or xenobionts, as for example, found in *Formicoxenus* (Myrmicinae) living in colonies of *Formica* (Formicinae) and *Myrmica* or *Manica* (Myrmicinae). Host and parasite in this group are morphologically very different (Stäger, 1925; Stumper, 1950; Francoeur et al., 1985; Lenoir et al., 1992). The evolutionary precursors for this type of parasitism however, are unclear at the moment, though plesiotropism (Wheeler, 1901) may be a good candidate. It is also unknown whether *P. lama* and *P. loweryi* have a common, already xenobiotic ancestor, or even whether all members of the *viehmeyeri*-group have more or less close parasitic relations to certain host species, or what systematic relations might link this group with other *Polyrhachis*-groups having associations with *Camponotus* or *Gnamptogenys* species (Maschwitz et al., 2000). Further comparative studies of species within and outside the *Polyrhachis viehmeyeri* group are necessary.

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## References

- Buschinger, A. and T.M. Alloway, 1978. Caste polymorphism in *Harpagoxenus canadensis* M.R. Smith (Hymenoptera: Formicidae). *Insectes Soc.* 25: 339–350.
- Francoeur, A., R. Loisel and A. Buschinger, 1985. Biosystématique de la tribu Leptothoracini (Hymenoptera: Formicidae). 1. Le genre *Formicoxenus* dans la région holarctique. *Nat. Can. (Que)* 112: 343–403.
- Kohout, R.J., 1990. A review of the *Polyrhachis viehmeyeri* species-group (Hymenoptera: Formicidae: Formicinae). *Mem. Qld. Mus.* 28: 499–508.
- Kohout, R.J., 1994a. *Polyrhachis lama*, a new ant from the Tibetan plateau (Formicidae: Formicinae). *Mem. Qld. Mus.* 35: 137–138.
- Kohout, R.J., 1994b. New synonymy of three Australian ants (Formicidae: Formicinae: *Polyrhachis*). *Mem. Qld. Mus.* 35: 135–136.
- Le Masne, G., 1956. Recherches sur les fourmis parasites. Le parasitisme social double. *C.R. Séances Acad. Sci. (Paris)* 243: 1243–1246.
- Lenoir, A., C. Errard, A. Francoeur and R. Loisel, 1992. Relations entre la fourmi parasite *Formicoxenus provancheri* et son hôte *Myrmica incompleta*. Données biologiques et éthologiques (Hymenoptera: Formicidae). *Insectes Soc.* 39: 81–97.
- Liefke, C., W.H.O. Dorow, B. Hölldobler and U. Maschwitz, 1998. Nesting and food resources of syntopic species of the ant genus *Polyrhachis* (Hymenoptera: Formicidae) in West-Malaysia. *Insectes Soc.* 45: 411–425.
- Liefke, C., B. Hölldobler and U. Maschwitz, 2001. Recruitment behaviour in the ant genus *Polyrhachis* (Hymenoptera: Formicidae). *J. Insect Behav.* 14: 637–657.
- Maschwitz, U., W.H.O. Dorow, A. Buschinger and G. Kalytta, 2000. Social parasitism involving ants of different subfamilies: *Polyrhachis lama* (Formicinae) an obligatory inquiline of *Diacamma* sp. (Ponerinae) in Java. *Insectes Soc.* 47: 27–35.
- Stäger, R., 1925. Das Leben der Gastameise (*Formicoxenus nitidulus* Nyl.) in neuer Beleuchtung. *Z. Morphol. Ökol. Tiere* 3: 452–476.
- Stumper, R., 1950. Les associations complexes des fourmis: commensalisme, symbiose et parasitisme. *Bull. Biol. Fr. Belg.* 84: 376–399.
- Wheeler, W.M., 1901. The compound and mixed nests of American ants. Part I+II. The known cases of social symbiosis among American ants. *Am. Nat.* 35: 513–539.

## Appendix

In a 3 weeks expedition to the former collecting sites of members of the rare *P. (Myrmhopla) viehmeyeri* species – group in Queensland, Australia we dug out as many *Rhytidoponera* nests as possible to check whether they were inhabited by *Polyrhachis* species. The following sites were visited:

| Collecting site | Original locality of | Findings  |  |
|-----------------|----------------------|---|--|
|                 |                      | <i>Rhytidoponera</i>  | <i>Polyrhachis</i>   |
| Collinsville    | <i>P. rustica</i>    | unidentified species A, 1 col.<br>unidentif. species B, 15 col.   | no <i>Polyrhachis</i>                                      |
| Mareeba         | <i>P. rustica</i>    | unidentif. species, C, 21 col.  | no <i>Polyrhachis</i>                                      |
| Marlborough     | <i>P. eremita</i>    | no <i>Rhytidoponera</i>   | no <i>Polyrhachis</i>                                      |
| Miles           | <i>P. loweryi</i>    | 10 col. belonging to the <i>aciculata</i> species-group<br>5 col. belonging to the <i>convexa</i> species-group | 6 col. <i>Polyrhachis loweryi</i><br>no <i>Polyrhachis</i> |

First experiments were carried out in the field and in large plastic vessels. Thereafter the studies were continued in the laboratory.



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