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Research article

When David and Goliath share a home: Compound nesting of *Pyramica* and *Platythyrea* ants

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Abstract. We documented a commensal association between two phylogenetically distant ant subfamilies (Ponerinae and Myrmicinae). The host (*Platythyrea conradti*) and its tiny guest (*Pyramica maynei*) nest in the same hollow branches in West African forests. Brood chambers are adjacent but separate, and the guest scavenges on prey remains of the host, which may benefit from improved nest hygiene. Two mated dealate queens of *Pyramica* were collected in one small *Platythyrea* nest, suggesting that they can hunt (non-claustral foundation) in the safe environment provided. An experiment showed that the guest can survive alone and was able to hunt collembolans.

Keywords: Symbiosis, commensalism, *Platythyrea conradti*, *Pyramica maynei*, Dacetini.

Introduction

Ants show a tremendous diversity of social adaptations, that include frequent symbioses with plants, fungi, and insects including other ants (Hölldobler and Wilson, 1990; Schultz and McGlynn, 2000). Associations among ants range from weak and opportunistic between otherwise totally independent species, to extreme and obligate where a parasite species lacking the worker caste is fully dependent on its host (inquilinism). Two kinds of nesting symbioses have long been recognized in ants (Wasmann, 1891). In 'mixed nests' the brood of two species are mingled and reared communally. This generally occurs between closely related species (Emery, 1909; but see Maschwitz et al., 2000) and can lead to slavery or inquilinism. In 'compound nests', the brood of two species are kept separate but close, and interactions are often food-based, e.g. small ants build nests near those of larger species and either feed on refuse in the host middens or rob the host workers when they return home carrying food. Social parasitism is more marked when small species enter the nest chambers of their host to steal food and prey on their brood (Forel, 1901). This reaches an extreme when the parasite species is totally dependent on its host and gets food by regurgitation (Errard et al., 1997). However, contrary to mixed nests, species in compound nests are not necessarily closely related.

Hölldobler and Wilson (1990) listed 43 genera of social parasites belonging to five ant subfamilies, but not a single one in the phylogenetically basal Amblyoponinae and Ponerinae *sensu stricto* (Bolton, 2003). However in recent years social parasitism has been documented in Ponerinae by several researchers (Orivel et al., 1997). In Java, *Diacamma* sp. is involved in a mixed nest with *Polyrhachis lama* (Maschwitz et al., 2000), as well as a compound nest with *Strumigenys* sp.1 (Kaufmann et al., 2003). *Diacamma* sp. 2 hosts *Pheidole* sp. 21, and *Pachycondyla* sp.1 hosts *Strumigenys* sp.3 (Kaufmann et al., 2003). Another association was described between *Rhytidoponera* and *Polyrhachis loweryi* (Maschwitz et al., 2003). Here we report a new case of compound nesting between two phylogenetically distant species. The guest *Pyramica maynei* (previously called *Strumigenys maynei* and *Serrastruma maynei*; Bolton 2000), is in the tribe Dacetini (Myrmicinae). It occurs in African tropical forests, reaching down to South Africa (H. Robertson, pers. comm.). This tiny ant (2.5 mm long) nests with the

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much bigger Ponerinae ant *Platythyrea conradti* (15 mm long) in hollow tree branches.

Material and methods

Twelve colonies of *P. conradti* were collected in gallery forest along the Bandama River in Lamto Ecological Station, Ivory Coast (6°13' N, 5°01' W), during December 2001 (5 colonies), April 2002 (4 colonies) and June 2002 (3 colonies). Whole branches containing the nests were sawn off and opened in the laboratory in order to avoid ants escaping. The two species were housed in plaster nests with glass roof and maintained humid at 25°C. Some organic debris from the original nests were also added. Food was given daily outside the nest: mealworm pupae or larvae, small crickets, diluted honey and occasionally collembolans. The ants were observed under a Leica MZ6 stereomicroscope.

Results

A *Pyramica* colony was present in 9 of the 12 *Platythyrea* nests. The latter (107 ± 66 workers) inhabit large cavities inside living trees (description in Lévieux, 1976). *P. maynei* has its own network of small galleries on the periphery, in the rotten sapwood, with connections to *P. conradti*'s cavity. Arboreal dacetines are exceptional (Bolton, 2000), and all previous reports of social parasitism in this tribe involved ground-dwelling hosts.

In the field, 20 nest entrances of *P. conradti* were observed (15 minutes each) during dry and rainy seasons in order to check the foraging activity of both *P. conradti* and *P. maynei*. Nest entrances are 1–2 meters above ground, and constructed with soil and vegetal debris. During the dry season, few *P. conradti* workers left their nest to forage. Likewise, *P. maynei* workers were only seen outside 2 of the 20 nests. However during the rainy season, *P. conradti* hunted actively (e.g. small moths, small flies, crickets) in the tree canopy, and several *P. maynei* workers walked outside the entrance of 15 out of the 20 nests checked. They were never seen further away than 10 cm from the entrances.

We collected two dealate inseminated *P. maynei* queens inside a small *P. conradti* colony consisting of one queen, 24 workers, eggs, small larvae but no cocoons. This colony size is much lower than the average of 99 ± 66 workers (Molet and Peeters, 2006), suggesting that *Pyramica* foundresses can locate colonies of their host soon after initiation. In the laboratory these two queens settled separately in two tiny gaps of the plaster nest and laid eggs. They foraged in *P. conradti*'s chambers, and even hunted collembolans which they fed to their first larvae. One of the queens died early, but the larvae of the other developed into pupae and workers.

In the laboratory, *P. maynei* nested in gaps between the glass roof and the plaster walls, while *P. conradti* remained in the main chambers. *P. maynei* used soil particles to build a wall all around its nest, with distinct exits leading into *P. conradti*'s chambers. *P. maynei* colonies (n=3 reared in the laboratory for several weeks) had 300 to 400 workers and a single dealate mated queen. Winged gynes and many winged males occurred in some colonies. The dealate queen usually stayed close to the eggs and young larvae, but she sometimes wandered through the nest. She behaved aggressively and bit workers. Workers were timid and fled her. In contrast, males approached her without being aggressed. When *Platythyrea* workers brought back prey inside the nest, they dismembered it so that larvae and adults could feed directly. Many *Pyramica* workers regularly foraged in the main chambers, searching for tiny remains of *Platythyrea*'s prey and carrying these back to their own chambers. However they rarely walked among *Platythyrea* adults or brood. They scavenged *Platythyrea* corpses, retrieving pieces of cuticle with tissues still attached. We have more than ten observations of *Pyramica* workers feeding directly from fresh prey of *Platythyrea*. In this case, some *Platythyrea* workers rushed toward the most daring *Pyramica* foragers, positioned them between their mandibles with antennal hits, lifted them, carried them elsewhere and put them back on the ground (Fig. 1). The *Pyramica* workers were never injured and soon resumed foraging.

When housed in artificial nests without their host, *P. maynei* survived and continued to produce brood and adults. The foragers caught live collembolans, in the typical way of ground-foraging *Pyramica* species (Dejean, 1983). Once a collembolan was sufficiently close to a *P. maynei* worker, she turned around to face the prey and rushed towards it with opened mandibles. The prey was seized either on the body or on an appendage and immediately stung. It was brought back to the nest and given to larvae or shared among workers. We never saw the queen feeding on the prey.

Discussion

The biology of *Pyramica maynei* suggests that it enjoys a commensal relationship with *Platythyrea*. The two species frequently occur together, although we do not know whether *P. maynei* remains able to nest independently. The brood of both species are kept completely separate. *P. maynei* scavenges food from *P. conradti*'s chamber, as in the association between *Pheidole* and *Dinoponera* (Paiva, 1993), and between *Pheidole* sp. 21 and *Diacamma* sp. 2 (Kaufmann et al., 2003). This behaviour may help clean the nest. *P. conradti* workers are generally indifferent to their guest, except when the latter attempts to feed on fresh prey; the host removes them without injury or death. Moreover *P. maynei* was never observed to prey on *P. conradti*'s brood, unlike *Strumigenys* sp.1 with *Diacamma* sp.1 (Kaufmann et al., 2003). In addition to recycling food from *P. conradti*, *P. maynei* catches prey near the entrance of *conradti*'s nest. Indeed, the accumulation of organic debris used to build the entrances may be colonized during the rainy season by collembolans. These facts suggest that the association is beneficial to *P. maynei*,

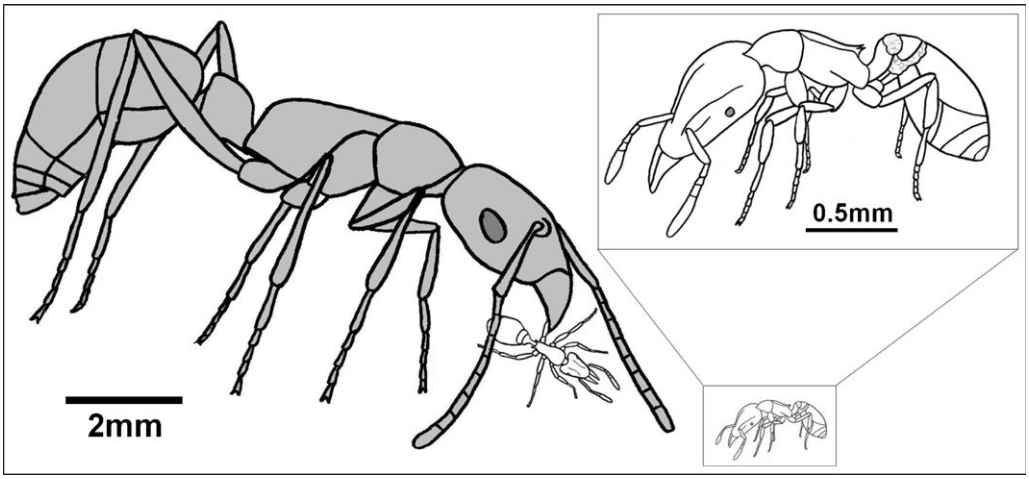

Figure 1. A *P. conradti* worker (in grey) carries a *P. maynei* worker (in white) away from a freshly killed prey.

which is provided with food inside a protected area and with a quality hunting area close to the entrance of the host nest. Thus workers seldom need to forage on the tree trunk. The association seems neutral or even beneficial to *P. conradti*, the nest of which is cleaned and thus less likely to be invaded by micro-arthropods (the wooden substrate is often very humid). However, comparative data on *P. conradti* nests with and without *Pyramica* are needed to verify this benefit. Note that our observations were carried out under conditions of *ad libitum* food supply, and we cannot rule out that when food gets scarce, the guest looks for food more aggressively.

There may also be an important benefit to incipient *P. maynei* colonies, because the non-claustral foundresses can forage without taking risks outside the *P. conradti* nests. Founding queens in other Dacetini need to forage outside the nests (Dejean, 1987) and are thus exposed to predation and accidents. We do not know how *P. maynei* queens locate *P. conradti* nests. They might either search for typical hollow branches, or emigrate with *P. conradti*. New colonies of *P. conradti* are founded by fission (Molet and Peeters, 2006). It is known that *Pheidole* sp.21 queens can find *Diacamma* sp.2 colonies (Kaufmann et al., 2003), but it is more difficult to locate nests of a tree-living species as opposed to a ground-dwelling species.

Ants in the genus *Pyramica* usually live freely and nest in the ground. Like all Dacetini species, they are predators. They forage in the litter for collembolans that they slowly approach, catch with their short 60 degrees-opening mandibles, and immediately sting (Dejean, 1983; Masuko, 1984). *P. maynei* show many characters of these free-living ants since workers retain the ability to hunt collembolans, and so do the queens during non-claustral colony foundation. This is unlike a *Pyramica* (= *Kyidris*) that is a temporary social parasite of *Strumigenys*, and in which founding queens exhibit a regression of hunting ability (Wilson and Brown, 1956).

The scarcity of known social parasites in the Ponerinae appears to be a reflection of relatively little fieldwork done in tropical regions. Although the lack of trophallaxis among nestmates (Peeters, 1997) means that they cannot be exploited by parasites in this way, their habit of hunting and retrieving large pieces of prey seems to make them an attractive target for scavengers. Dacetini often seem to be involved, and the huge difference in size contributes to facilitate coexistence (as in the associations studied by Kaufmann et al., 2003).

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