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Notes on the biology of Brazilian ant populations of the *Pachycondyla foetida* species complex (Formicidae: Ponerinae)

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Abstract
In ant taxonomy, biological studies are especially important to complete the information aiming to identify species belonging to unresolved or confused taxa. Such observations allow the inclusion of biological data with other characteristics of the determined group, something that preserved specimens in collections do not reveal, such as nesting site, foraging time, nuptial flight and especially the relationship between castes, in support of taxonomic analysis and descriptions. Here, nests of three species of the complex *P. foetida* were observed and collected in three Brazilian localities. Pleometrosis, secondary monogyny and cannibalism were observed for the ant *P. inversa*. In many ant species, newly mated queens associate with other queens to establish new colonies, independent of parenthood. In the ant genus *Pachycondyla*, the reproductive structure varies broadly and aggressiveness seems to be an important factor in structuring the organization and reproductive division in the colony. The occurrence of males in nests of *P. inversa* and *P. curvinodis* also allowed the description of males. The nuptial flight period was estimated to be August for *P. inversa*, October for *P. villosa* and November for *P. curvinodis*.

Introduction

In the ant genus *Pachycondyla* Smith, the reproductive structure varies widely and aggressiveness seems to be an important factor in structuring the organization and reproductive division in the colony (Trunzer et al., 1998; D'Ettorre et al., 2005). Cooperation among individuals in the same social group or in the same family exists in several species, which in some cases results in the abdication of their own reproduction to devote themselves to the care of offspring of other individuals from the group. This system can involve a relationship of dominance and subordination (Walters et al., 1992; Hatchwell & Komdeur, 2000; Kokko et al., 2000; Griffin & West, 2002).

In many ant species, newly mated queens can associate themselves with other queens to establish new colonies independent of parenthood (Hagen et al., 1988; Sasaki et al., 1996). In some cases, workers become reproductive and establish hierarchies of dominancy by aggressiveness in situations where the queen is removed from the nest (Heinze et al., 2002).

The genus *Pachycondyla* has a pantropical distribution with 380 species and subspecies known (Bolton, 2012). Mackay & Mackay (2010) revised the genus for the New World. In the same study the genus was divided into several complexes of species based on morphological characters; 18 are recognized in the New World, among them the *P. foetida* complex. Fernandes et al. (2014) revised the *P. foetida* complex for Brazil, and added two new species for the Neotropical Region, which currently has 94 species.

Today, the *P. foetida* complex comprises the second largest in number of species within the genus, with 13 species recorded in the New World and seven in Brazil: *P. bactronica* Fernandes et al., *P. billemma* Fernandes et al., P. curvinodis Forel, *P. villosa* (Fabricius), *P. inversa* (Smith), *P. foetida* (Linnaeus), and *P. theresiae* Forel" (Fernandes et al., 2014).

According to Mackay & Mackay (2010), individuals of *Pachycondyla curvinodis* from Nicaragua were collected in the rotten parts of a living tree behind a termite nest of *Nasutitermes* Banks. Other specimens were collected in hollow stems of *Cecropia* sp. in Costa Rica and in a tree canopy sprayed with insecticide in Peru.

Pachycondyla villosa is the most nominally cited species within the *P. foetida* complex (Camargo-Mathias & Caetano, 1991; Camargo-Mathias et al., 1991; Camargo-Mathias & Caetano, 1992a; 1992b; 1995a; 1995b; 1996; Mariano et al., 2000; Trunzer et al., 1998; Lachaud et al*.,* 1984; Hölldobler, 1985; Dejean & Corbara, 1990a, 1990b; Dejean et al*.,* 1990; Valenzuela-Gonzalez et al., 1994; Dejean & Corbara, 1998; Dejean, 1990).

Like other members of this group, *P. villosa* has arboreal habits, nesting in trees. It forages on the ground or in trees, looking for extrafloral nectaries or exudates of mealybugs, and can carry drops of liquid between its jaws (Hölldobler, 1985; Paul & Roces, 2003). The colonies are established in hollow logs and in epiphytes (Dejean et al., 1990; Dejean & Olmsted, 1997) at the base of *Tillandsia bulbosa* Hook and *Tillandsia streptophylla* Schweid (Dejean et al*.,* 1995) and in orchid pseudobulbs such as *Schomburgkia tibicinis* Batem (Wheeler, 1942). They are occasionally found in *Cecropia* spp., especially in *Cecropia hispidissima* Cuatrec and in cavities of *Bursera simaruba* (L.) Sarg. (Dejean et al*.,* 1992).

Pachycondyla inversa (Smith) nests have been found in rotten cocoa pods and holes in cocoa trees (*Theobroma cacao* L.) and in rotten pods lying in the litter (Heinze, et al., 2001; Kolmer & Heinze, 2000). Workers forage under sheets of *Byttneria aculeata* Jacq. (Sterculiaceae). The queens can cooperate during colony establishment (Kolmer & Heinze, 2000; Tentschert et al., 2001) and thus form polygynous nests (Heinze et al*.,* 2001). Several studies have indicated that colonies of *P. inversa* may be founded by a single (haplometrose) or several (pleometrose) queens and may also result in polygynous colonies (Trunzer et al., 1998; Heinze, 1993; Heinze et al., 2001; Kolmer et al., 2002; D'Ettorre et al., 2005).

Specimens of *P. foetida* has been collected in the canopy by fumigation (Mackay & Mackay, 2010: 335). John Longino also collected *P. foetida* workers in a *Hieronyma oblonga* (Tul.) Mull. Arg. tree recently felled in La Selva, Costa Rica. The tree had a small nest entrance hole, little larger than a worker, leading to a large cavity in a knot, where there were abundant workers (Longino's website http://academic.evergreen.edu). *Pachycondyla theresiae* occurs in wet forest habitats. Workers forage in the low arboreal zone and in extrafloral nectaries of *Passiflora* (Passifloraceae), (Longino's website http://academic.evergreen.edu). The aim of this study was to add information about the natural history of Brazilian populations of the *P. foetida* species, with data about nesting sites, foraging schedules, nuptial flight period, and reproductive organization in the colony, something that preserved specimens in museum collections are unable to reveal.

Material and Methods

The nest of *P. villosa* was obtained in Itacoatiara city, on the São Francisco property (03°06'16.6"S 58°28'44.0"W), in October 2009. The nest of *P. inversa* was collected near Manaus city, in Adolpho Ducke Forest Reserve - RFAD (02°55'46.9" S 59°58'28.5"W), in August of 2010. Both cities are located in the state of Amazonas. The nest of *P. curvinodis* was obtained in Campinas city, in the Mata de Santa Genebra (22°49'32.9" S 47°06'17.7"W), in November 2009, in the state of São Paulo.

Further observations were performed in the laboratory under controlled temperature (26° C) and relative humidity (60% ± 30%). Nests were kept in BOD incubators within plastic trays (33 x 25 x 11 cm) with a gypsum background (2 cm thickness). We used a 10% solution of honey and water to feed adults (0.5 ml) once a day. The larvae were fed with immature beetles (Coleoptera: Tenebrionidae) three times a week.

All nests were discovered after locating a single worker (*P. villosa* and *P. curvinodis*) or queen (P. *inversa*) on litter, which was then followed up to the entrance of the nest. The number of individuals of each caste (males, queens and workers) was recorded for each nest collected and the tree species was identified, whenever possible, as well as the nest structure. After these field observations, the nests were completely removed with the aid of forceps and shovel, and photographed during this process to record the behavior of the ants and aspects of the nest.

Voucher specimens were deposited in the Invertebrate Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA) and duplicates were deposited in the Collection of the Laboratório of Mirmecologia do Centro de Pesquisas do Cacau (CPDC), all in Brazil.

Results

Pachycondyla curvinodis Forel

A total of 95 individuals, with 85 workers, nine males and one queen of *P. curvinodis* were obtained from one nest in Mata de Santa Genebra located about 1 meter above the ground in the cavity of a palm of the genus *Syagrus* (Cham.) Glassman (Fig. 1A-D). The observations began at around 8 a.m. with an air temperature of around 25°C and 53% relative humidity. One foraging ant was observed and followed to the nest until 9 a.m. before we started to remove the nest.

The nest was divided into four chambers: the upper chamber had the nest entrance, the two intermediate chambers were used for the raising of larvae and pupae, and the lower chamber was used as a dumping ground for insect bodies and pupae wrappers (Fig. 1B-C).

The ants did not show any aggressive behavior during the opening of their nest. The workers carried males in their

jaws to lower nest levels, but again did not show any kind of aggressive reaction when we removed the males (Fig. 1D).

We collected five males with yellow gaster and legs and four with black gaster and legs, a character hitherto observed only in males of *P. villosa* by Mackay & Mackay (2010). The field collection expanded the occurrence of *P. curvinodis* to Brazil.

Pachycondyla villosa (Fabricius)

A total of 67 ants, 41 workers, 25 males and one queen of *P. villosa* were collected near Itacoatiara. We began our observations at around 1 p.m., with air temperature around 36˚C and 51% relative humidity, but no foraging activity was observed until 4 p.m. We found the first ant foraging in the litter after 4 p.m., the time at which the temperature had decreased to about 30° C and the humidity increased to 63%. The ant was followed up to the nest entrance located on a *Leopoldinia piassaba* Wallace palm tree measuring approximately 16 meters in height (Fig. 2A-B).

In the early evening the nest was removed to count individuals and observe its structure (Fig. 2B). During the removal, the workers were quite aggressive and carried out males in their jaws as observed in *P. curvinodis*. No eggs, larvae or pupae were observed in the nest.

Pachycondyla inversa (Smith)

A nest of *P. inversa* was located inside a hollow twig and observed for three consecutive days in the Adolpho Ducke Forest Reserve. During the observation the queen showed some periodicity with respect to foraging time, starting at around 6 p.m., with an average temperature of 30˚C and 60% relative humidity in the evening. On the third day, at 5:33 p.m., a queen with an alar scar was observed entering into the same hollow twig, where there was a second queen (Fig. 3A). The twig contained three eggs maintained by one queen in her jaws during removal of the nest while the other queen occupied the entrance (Fig. 3B). We also found two pre-pupae of *P. inversa* and two heads, a mesosoma and a gaster of *Camponotus* sp. in the nest.

Fig. 2 – Nest of *P. villosa* (Fabricius): (A) Nest in palm *Leopoldinia piassaba* Wallace; (B) Nest chambers.

This nest was taken to the laboratory, where we could observe that one queen had lost one antennae and one median leg. It was found dead the following day. After her death, the second queen assumed the function of oviposition (Fig. 3B-D); for seven months the surviving queen oviposited male offspring only in a B.O.D incubator where the colony was maintained (Fig. 3E-F).

We believe that the exclusive oviposition of males by this second queen was related to an absence of fecundation. A total of 18 *P. inversa* males were obtained; counting of eggs, larvae, pupae and pre-pupae was performed daily. We noticed that some eggs were regularly lost; this led us to believe cannibalism of male eggs was occurring, which were offered by the queen to larvae or were consumed by the queen. The pupae emerged only during the night. The males survived for an average of four days after their emergence, after which they died.

Unfortunately, we were unable to obtain specimens of *P. foetida* and *P. theresiae* in our fieldwork, despite many attempts.

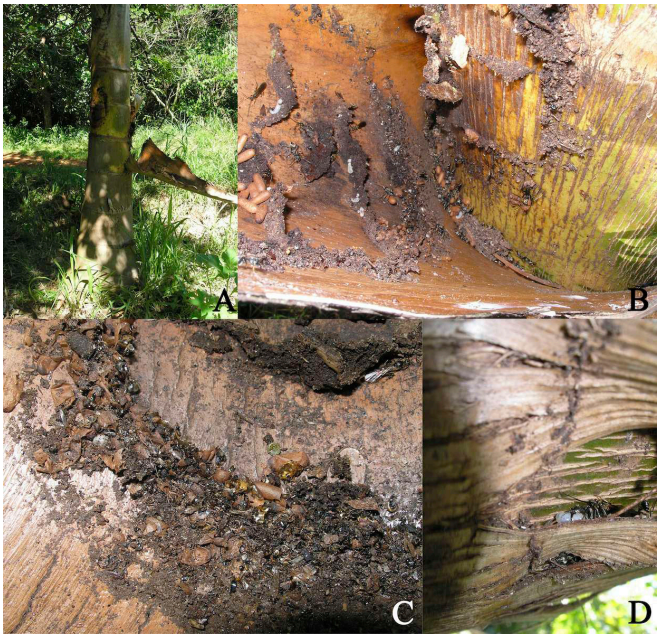

Fig. 1 – Nest of *Pachycondyla curvinodis* Forel: (A) Palm of genus *Syagrus* sp.; (B) Nest chambers; (C) Lower chamber; (D) Adult of *P. curvinodis* carrying the larvae.

Discussion

We observed a variation in the tegument of the legs and gaster (black or yellow color) of *P. curvinodis* males. This variation was also reported for males of *P. villosa* by Mackay and Mackay (2010: 573).

Another fact reported by Mackay and Mackay (2010)

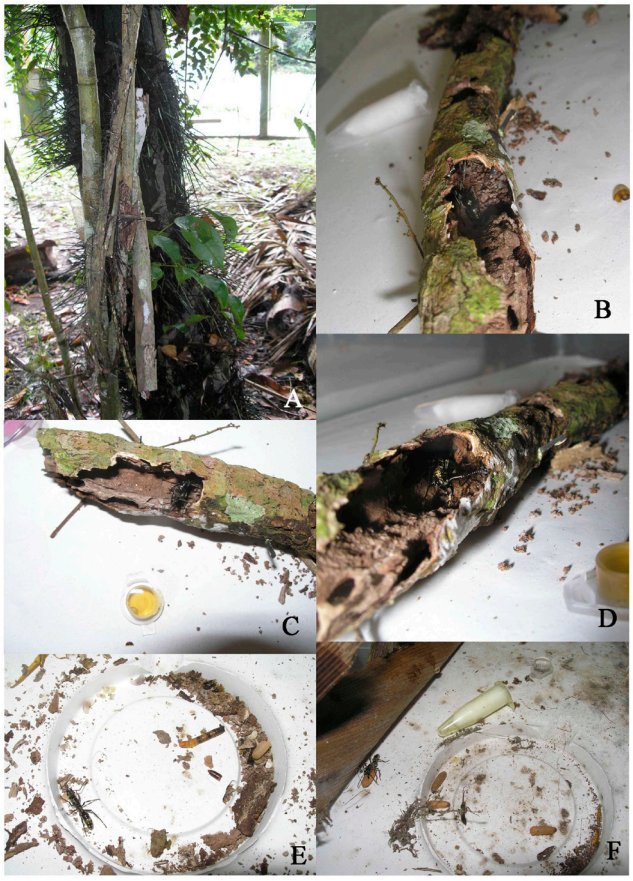

Fig. 3 – Nest of *Pachyocnyla inversa* (Smith): (A) Nest (hollow twig) in the tree; (B) Nest with two queens and your eggs; (C) Queen without a median leg and one antennae; (D) Nest in laboratory; (E) Queen caring the offspring; (F) Males, pupae and eggs of *P. inversa*.

is that *P. curvinodis* does not occur in Brazil, although it was recorded in the states of Espírito Santo and Rio de Janeiro by Forel (1901: 45 and 1907: 1, respectively). We confirmed the occurrence of this species in Campinas city (São Paulo state), in Brazil.

As Valenzuela-Gonzalez et al. (1994) also observed, *P. villosa* has its main foraging activity during the night, when the humidity is high and the temperature low. *P. villosa* demonstrates strong allegiance to a particular area and does not practice recruitment (Fresneau et al., 1982; Lachaud et al., 1984; Fresneau 1985). *P. villosa* is considered the most aggressive species in the *P. foetida* complex, and this behavior seems related to its habit of predation and nest defense (Maes, 1989; Dejean et al*.,* 1990; Wild, 2005). Species such as *P. curvinodis* and *P. inversa* showed less aggressiveness compared to *P. villosa*.

Founding queens of *P. inversa* form a social hierarchy system mediated by aggressive interactions; the queen placed lowest in the hierarchy is responsible for foraging, while the other queens are egg layers (Heinze, 1993; Heinze, et al., 2001; Trunzer et al., 1998; Kolmer & Heinze, 2000; Kolmer et al., 2002; D'Ettorre et al., 2005). The absence of one antennae and median leg of one queen may have been the consequence of a fight for nest dominance. This mode of colony establishment reduces the risks to which the queens are exposed, since before emergence of the first workers, the queen feeds the larvae with her own body tissue and/or leaves periodically to forage (D'Ettorre et al., 2005).

Normally, after the first workers emerge, one of the queens is expelled or killed by the other queen, resulting in secondary monogyny (Hölldobler & Wilson, 1977; 1990; Rissing & Pollock, 1988; Heinze, 1993; Choe & Perlman, 1997). In the case of *P. inversa,* one queen was found dead on the following day (04.viii.2010), and no worker was born during the period of breeding.

Cooperation among queens in the phase of colony establishment has been described in other species of the genus *Pachycondyla,* such as *P. marginata* Roger (Leal & Oliveira, 1995) and *P. villosa* Fabricius (Heinze et al., 2001). Although all the queens are able to oviposite eggs, this hierarchy determines the quantitiy of eggs oviposited; the dominant queen may also destroy the eggs of subordinates (Trunzer et al., 1998; Kolmer & Heinze, 2000; Kolmer et al*.,* 2002). Moreover, the best-placed queen in the hierarchy may eat the eggs produced by the other queens (Kolmer & Heinze, 2000; D'Ettorre et al., 2005).

Oophagy (egg cannibalism) is indispensable to the social Hymenoptera (Wilson, 1971). In social insects, egg cannibalism may be associated with competition for reproduction. This event seems restricted to some genera in the subfamily Ponerinae. Some eggs of *P. inversa* disappeared from the nest during the nocturnal period, indicating that they were offered to larvae or to the dominant queen.

The cannibalism observed in *P. inversa* may be an adaptive response (Driessen et al., 1984), concentrated during periods when insect prey is in short supply.

In *Pachycondyla obscuricornis* Emery the destruction of unfertilized eggs (trophic eggs) by the queen and/ or workers is relatively common (Rodrigues et al., 2011). Trophic eggs (eggs that cannot develop but are used exclusively as food) are characteristically flaccid or differ in shape from reproductive eggs (Hölldobler & Wilson, 1990). The morphological differences were described in the closely related species *P. villosa* (Camargo-Mathias & Caetano, 1995b). In ants they are produced by workers or virgin queens and constitute an efficient transfer of resources within the colony (Elgar & Crespi, 1992). Thus ant queens may enhance their individual fitness by eating trophic eggs and through that gain higher energy input. On the contrary, queens never eat reproductive eggs in the context of resources and such behavior is usually interpreted as policing.

The consumption of trophic eggs is distinct from the cannibalism of reproductive eggs occurring in some permanently queenless ponerine ants (Peeters & Tsuji, 1993; Monnin & Peeters, 1997). In *Pachycondyla apicalis* (Smith), trophic eggs are laid for the workers and are immediately offered to the queen (Dietemann & Peeters, 2000). These may be her main food source, since she seldom feeds on pieces of prey.

In conclusion, this study added information about *P. inversa,* including nesting sites, the social hierarchy system, mediated by aggressive interactions, the relationship of dominance and subordination, the founding of nests by two queens (pleometrosis) resulting in secondary monogyny, and oophagy (egg cannibalism). Nesting sites, foraging schedules, and identification of the nuptial flight period for *P. inversa* (August), *P. villosa* (October), and *P. curvinodis* (November), are further examples of important information that preserved specimens in museum collections cannot reveal.

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