

Research article

Parabiosis between basal fungus-growing ants (Formicidae, Attini)

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Abstract. We describe the first observation of parabiosis between two Attini ants (*Apterostigma urichii* Forel and *Cyphomyrmex faunulus* Wheeler) found in northern Manaus, AM, Brazil. Complete, mature colonies of both species were found in a single cavity inside a rotten log, sharing and tending a single combined fungus garden, made up of two distinct halves, each cultivated by one species. Workers of one species often antennated workers of the other species and showed no aggression toward each other or toward each other's workers, queens, or immatures. Laboratory observations suggest that immatures of both species feed on hyphae from either half of the fungus garden. We were not able to find other parabiotic pairs involving the same species in the same locality, although we found colonies of both species sharing trails and foraging territories.

Keywords. Parabiosis, basal Attini, ants, fungus-growing.

Introduction

Parabiosis is defined as a particular form of facultative or obligatory symbiosis in which two or more species utilize the same nest and sometimes even the same odour trails, but nevertheless keep their broods separate (Hölldobler and Wilson, 1990). It was first described by Forel (1898), based on his observations of the association between *Crematogaster limata parabiota* and *Dolichoderus debilis* in Colombia. Forel (*op. cit.*) emphasized the facultative nature of this particular association, pointing out that, in general, neither of the participating species is dependent on the association; although parabiotic species often live together, they may also be found nesting

and living independently. However, in some cases, the relationships between parabiotic species are not necessarily amicable and mutualistic, but instead may be parasitic, with one of the species driving away the other at the food source (Swain, 1980).

Parabiosis has been described for ant species from all over the globe (e.g. Santschi 1910; Greaves and Hughes, 1974; Greenslade and Haliday, 1983; Kaufmann and Maschwitz, 2006), but most records of this association report facultative relations and are concentrated in the Neotropics, where several parabiotic ant associations, generally involving members of different subfamilies, have been recorded (Mann, 1912; Wheeler, 1921; Weber, 1943; Orivel et al., 1996; Davidson, 1988; Ipinza-Regla et al., 2005). Until now, the only case of parabiosis between ants belonging to the same subfamily, but to different tribes, involves the Formicinae *Brachymyrmex* and *Camponotus* (Errard et al., 2003). We describe here the first observation of parabiosis between two closely related ant species, of *Apterostigma* and *Cyphomyrmex*, both fungus-growing ant genera belonging to the tribe Attini (Myrmicinae).

Most fungus-growing ants are obligatory cultivators of basidiomycete fungi, on which they depend for nourishment (Hölldobler and Wilson, 1990). Recently, Mikheyev et al. (2006) challenged the paradigm that fungus-growers ecological success depends largely on ancient fungus vertical transmission allied to suppression of fungal sexuality. Green et al. (2002) and Mikheyev et al. (2006) were able to show evidence of frequent cultivar recombination in sympatric attines and long-distance horizontal transmission of symbionts independent of their ant hosts. As in most well characterized mutualisms, the general principle shifted from one-to-one specificity to diffuse coevolution between participants. Mikheyev et al. (2007) show that garden exchange likely happens continuously at the population level. However, no behavioural mechanism enabling the ants to either switch to a different

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cultivar or regain their cultivar after loss has been clearly identified thus far. In nature, fungus garden loss is due to pathogens or other causes. Experimentally, loss of the fungus garden induces fungus-growing ants to obtain a replacement cultivar from a neighbouring colony, either by joining the other colony and cooperating in the cultivation of a common garden, or by stealing or aggressively usurping a neighbour's garden (Adams et al., 2000).

Additionally, fungus-growing ants may share nests with non-attine ants, at least temporarily. Adams et al. (1998–1999; 2000) discovered colonies of *Megalomyrmex wettereri* Brandão in Panama containing healthy fungus gardens of *Cyphomyrmex longiscapus*; laboratory observations revealed that the *Megalomyrmex* “consume the fungus by cropping mycelium from the garden substrate. However, they do not forage for and add nutrient substrates, or otherwise tend the fungus garden; thus, when the garden becomes depleted, *M. wettereri* must locate and usurp new gardens in other attine colonies”. Other *Megalomyrmex* species of the *Silvestrii* species group have been found within the fungus gardens of various basal Attini (Brandão, 2003).

Attini is a diverse array of predominantly Neotropical genera (13 accepted as valid presently), which have been traditionally (and artificially) divided into the “Lower” attines, sometimes called basal, which includes the so-called Paleoattini (*Apterostigma*, *Mycocepurus* and *Myrmicocrypta*) and six genera of unknown affinities, and the Neoattini (also known as the “Higher” attines), which includes the leaf cutting *Atta* and *Acromyrmex*, and, for some authors, *Trachymyrmex* and *Sericomyrmex* as well. The Lower Attini live in colonies with at most a few hundreds of workers, in simple nests, whereas the Higher attines live in much larger colonies inhabiting complex nests. In general, basal Attini display little or no inter- or intraspecific aggression towards other ant species sharing their foraging territories, as already pointed out by Weber (1941), who noted how closely together different basal fungus-growing species may nest. Because basal Attini use very abundant organic detritus as substrates for fungus gardening, including pieces of arthropod carcasses and faeces (Leal and Oliveira, 2000), and the species are generalist foragers, it is believed that competition for resources is very low among them, and thus that aggression is also low (Tallamy and Wood, 1986). The results of a study on the foraging ecology of attine ants in a Brazilian savannah, in special as to the seasonal use of fungal substrate (Passos and Oliveira, 2003), revealed that the basal attines are very opportunistic and utilize plant parts according to the phenology of the vegetation. These attines preferred to collect available items from nearby plants and always harvested the fungal substrate on the ground. Recently-fallen flowers and fruits comprised the major part of the fungus-substrate used by all genera studied there. Tougher plant parts, such as leaves and seeds, insect remains, and other material were also used by the ants, particularly in the dry season, probably

to compensate for the lower availability of flowers and fruits during this period. However, in the more derived leaf cutters *Acromyrmex* and *Atta*, which cultivate fungi on macerated fresh vegetation, competition for resources may be high, with consequent territoriality and aggression among neighboring colonies, which may escalate into deadly wars among colonies, as seen in several ant species (Hölldobler and Wilson, 1990).

Obligatory parabiosis has been described for several pairs of ant species, usually involving species from distant phylogenetic lineages. For instance, *Crematogaster limata parabiatica* (Myrmicinae) and *Camponotus femoratus* (Formicinae) share nests and the same trail systems, although they utilize different food resources (Hölldobler and Wilson, 1990). Species with similar resource requirements are potential competitors and so are not expected to enter into parabiotic associations.

Methods

One parabiotic colony of *Apterostigma urichii* Forel and *Cyphomyrmex faunulus* Wheeler was found by the first two authors in a rotten log cavity in the Reserva Dimona, Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF), northern Manaus, AM (02°20'S; 65°05'W), Brazil, between November 27 and 29, 2004. The collectors actively searched for more colonies of both species in Dimona Farm, Colosso Farm (02°24'S; 59°52'W) and Km 41 Reserve (02°26'S; 59°46'W), all administrated by PDBFF (Bierregaard et al., 2002). In four weeks of intense field work they found several colonies of *C. faunulus* and *A. urichii* nesting in isolation in the three localities, but no other parabiotic pair. They found, in the Colosso Farm, two more heterospecific pairs of the cited species nesting below the bark of two different tree logs, but in both cases each species occupying its own chamber, less than 30 cm apart of the other species chamber.

The parabiotic colonies and the unique fungus mass were transferred to an artificial nest constructed from two 10 cm² acrylic boxes linked by a plastic tunnel; one box served as the foraging arena and the other as the colony chamber. We offered as garden substrate ground dried orange rind, dried oats, and the frass of an *Urbanus* sp. butterfly (Hesperiidae), all of which were accepted by workers of both species. Unfortunately, the workers were unable to fully reorganize the fungus garden (see below), and its health rapidly declined after arriving in the laboratory; workers of both species began to die upon arrival in the lab. The colonies survived for one week in artificial conditions.

Observation

The *Apterostigma urichii* and *Cyphomyrmex faunulus* colonies living in parabiosis had one dealated queen each and contained, respectively, 23 and 16 workers, two and one males, and multiple larvae and pupae. The single fungus garden filled up almost half of the cavity, and was clearly divided into two distinct halves, a reddish one inhabited by *C. faunulus* and a greenish one inhabited by *A. urichii* (Fig. 1). Approximately one-third of the combined fungus garden showed signs of deterioration and contained no immatures. The garden substrate in both halves consisted of unidentified anthers, small seeds, and fragments of insect exoskeletons (elytra, heads, antennae, and wings). The total volume of the fungus garden was 350 ml and the total weight, including the ants from both colonies, was 120 g.

In the half of the garden occupied by *A. urichii*, we found the pupa of a Muscidae fly (*Helina* sp.), from which an adult emerged immediately after the arrival of the colony in the lab. However, the adult fly died soon after emergence and, because its features had not completely sclerotized still, species-level identification was impossible.



Figure 1. Double-origin combined fungus garden shared by *Cyphomyrmex faunulus* (left) and *Apterostigma urichii* (right) found at Reserva Dimona Projeto Dinâmica Biológica de Fragmentos Florestais – PDBFF northern of Manaus, AM, Brazil. Note at the left half, the *C. faunulus* dealate gyne (middle) and a worker (above) and, at the right half, a worker and larvae (behind and at the down corner) of *A. urichii*. Picture taken in the lab by Domingos J. Rodrigues.

As is typical for live-collected attine colonies, the fungus garden almost completely broke apart while being transported from the field to the lab. Ants of both species worked together to rebuild it, and even transported each other's immatures to the newly partially rebuilt fungus garden. We cannot assure that each species tended the immatures of the partner species, but our impression is that immatures of both species were fed and transported by workers of both species, based on the significantly greater size of the *Apterostigma* larvae, in relation to those of *Cyphomyrmex*.

Workers of both species frequently antennated each other and walked freely over each other's halves of the fungus garden. On several occasions, we observed a worker of *A. urichii* antennating the *C. faunulus* dealate queen. We never observed even a single instance of aggression between the species during the week in which they were maintained in the lab.

The heterospecific pairs found nesting very close in Colosso Farm tree logs, although occupied different chambers, shared natural trails formed by crevices below the bark of the rotting trunks. Examination of the logs suggests that workers of both species even visited each other nests, and also do not show any aggressive behaviour towards each other.

Discussion

Colonies occupying different nest chambers inside rotten logs can be easily mixed together when the log is opened in the field. We rule out this possibility in the present case and are sure that the co-occurrence of two basal attines in a single nest chamber does not represent a collecting artefact. The fact that complete colonies were sharing a unique fungus mass inside a single chamber, with a single entrance, and the lack of aggressiveness among workers of the two species, indicates that the parabiotic colony and the combined fungus garden were truly living together. Also, we had the opportunity to observe other heterospecific pairs of these species sharing trails, but living in distinct nests.

We reject also the option that we had found, by chance, a momentary raid of a parasite or lestopiobic (when colonies of a small species nest in the walls of a larger species and enter the chamber of the larger to prey on brood or to rob food, Hölldobler and Wilson, 1990) species attacking its host, because we found dealated reproductive females and mature males, along with immatures, in both colonies of the parabiotic pair; raids are normally conducted only by workers. Furthermore, we never observed these ants attacking each other, as would be the case if we had by chance found one of the species attacking the nest of the other.

It is important to distinguish the case described here from the sharing of a fungus garden induced by the loss of a garden, e.g., due to pathogens (Adams et al., 2000), in which the colony of one attine species invades another colony (conspecific or of another species or even genus) in order to acquire a replacement cultivar. In the case reported here, both cultivated fungi are assumed to have been present and to have together composed a combined fungus garden (see below). As expected from such distantly related fungi, each was distinct and the two were not fully integrated, either in natural or laboratory conditions, even if the recomposition of the fungus in the laboratory was only partial. According to Adams et al. (2000), usurpation involves the stinging and ultimately killing of the host species, contrariwise to the complete lack of aggressiveness between members of the different colonies we observed in the field and laboratory.

Apterostigma urichii belongs to the so-called Paleoattini and *Cyphomyrmex faunulus* is a basal member of the Neoattini. We would not expect leaf-cutters (derived members of Neoattini, *Atta* and *Acromyrmex*) to engage in parabiosis because leaf cutters compete for and defend their resources, resulting on territorialism, aggression, and even wars among neighbouring colonies. Even in permanent parabiotic relationships, there is a conflict of interest between partners (Vantaux et al., 2007) and one species can eject the other from the common nest (Swain, 1980). Because both *Apterostigma urichii* and *Cyphomyrmex faunulus* are commonly found nesting alone, the parabiotic association between them is obviously facultative. Similar facultative associations have been recorded between *Crematogaster limata parabiotica* and either *Pachycondyla goeldii* or *Camponotus femoratus* (Davidson, 1988; Orivel et al., 1996). If we accept the putative absence of competition among basal Attini ants, this absence *per se*, cannot fully explain the mutualistic relationship observed in the case described here. In addition to the requirement that both species do not compete for resources, the mutualism also requires that the association is selectively advantageous to both partners, which however, it is not always possible to ascertain. In the present case, favourable nesting sites could be limited (see Kaspari, 1996), leading these ants, that do not compete for foraging resources, to share nests, as they live in relatively small colonies and can not efficiently guard nesting sites. When nesting sites are the

limiting resource, *Solenopsis invicta* queens cooperate to found colonies pleometrotically (Tschinkel, 1998). Similar benefits derived from primary pleometrosis could help to explain the parabiotic association studied here, as, for instance, faster worker production in recently founded colonies and improved group defence against alien workers from mature colonies (reviewed in Hölldobler and Wilson, 1990). Besides the facultative nature of the observed parabiosis, the relation can also be only temporary.

The case described here is unusual because it involves a parabiosis between two ant species from two different genera that reportedly cultivate two very distinct fungal groups. *Apterostigma* species of the Pilosum group, which includes *A. urichii*, are exceptional among Attini in cultivating wood-decomposing (coral-mushrooms) Pterulaceae fungi (called G2 and G4), which are only distantly related to the litter-decomposing Lepiotaceae (Basidiomycota: Agaricales) that are universally cultivated by all other more than 200 species of fungus-growing ants, including the most basally diverging *Apterostigma* species in the Auriculatum group (Villesen et al., 2004). Cultivation of Pterulaceae represents a unique symbiont switch, with basal *Apterostigma* species retaining ancestral lepiotaceous fungiculture and with none of the monophyletic, pterulaceous-cultivating *Apterostigma* species known to have reverted back to lepiotaceous fungiculture. Munkacsi et al. (2004) showed that the Pterulaceae are morphologically and phylogenetic different from the Lepiotaceae, and discussed how the two fungi converged to the same evolutionary interactions with ants, despite their distinct origins.

The *Apterostigma urichii* gardens analyzed so far came from Kurupukari, Guyana, and are clearly veiled G2 fungus gardens hanging on tree trunks (Villesen et al., 2004). In general, G2 pterulaceous fungus gardens are protected by a mycelial veil, but when G2-cultivators nest in enclosed spaces (such as a chamber in a log or in the ground), the veil may be inconspicuous or easily damaged by the collector. Pterulaceous fungus gardens in the G4 group, in contrast, do not have veils. That is, the Pilosum group *Apterostigma* appears to grow the veil only in response to desiccation, or to partition off the garden in a larger space. In short, presence of a veil is a good indicator that the *Apterostigma* species is in the Pilosum group, but the absence of a veil does not necessarily mean that the ant does not belong to the Pilosum group nor that it is not cultivating a pterulaceous garden (Mueller, pers. comm.; Villesen et al., 2004). Attine ants are able to differentiate between closely related cultivar strains. Switches to distantly related cultivars are behaviourally unlikely, but, hypothetically, may occur under constrained conditions in which colonies are forced to import novel cultivars (Mueller et al., 2004).

The most surprising observation, however, is the combined nature of the fungus garden cultivated by the parabiotic colony. Unfortunately we were not able to culture it and we do not know whether or not the two

garden halves consisted of the same or of closely related fungi in the Leucocoprineae or whether they consisted of two very different fungi, one in the Pterulaceae and one in the Leucocoprineae. It is reasonable to expect that such distantly related fungi, when brought into contact, would have antagonistic reactions to each other, "battling" with antibiotic chemicals produced by different bacterial strains, which would result in reduced garden productivity (Lenoir et al., 2001). In nature, the unique fungal mass reared by the parabiotic colony presented clearly two halves distinct by different colours, even when observed in different lightning and shades. Although the ants were not able to fully recompose the fungal mass after transport to the laboratory, they tried to do so, and the partially recomposed fungus also presented the two very distinguished halves in laboratory conditions (Fig. 1). If we accept the hypothesis that the fungal mass actually belongs to a single fungus species, the two different colours could be the result from the ants adding different substrates for the same fungus in each one's half, which would imply in fungus malleability regarding substrate. If the fungus mass is the result of two combined fungus species, each one brought and reared by one of the ant species, this would imply in the compatibility of fungi from very different origins, and may thus represent an important observation in the context of the evolutionary history of the fungus-ant associations understanding.

Even if parabiosis between other pairs of basal attines has not been registered until now, it may be common. For example, Dr. Ulrich Mueller (pers. obs.) recorded two attine species, both in the genus *Mycocepurus*, which also live together. MacKay et al. (2004) briefly mentions that *Mycocepurus curvispinosus* apparently lives within nests of *M. smithii*, in Veracruz, Mexico, with whom they share trails with. The purpose of the present report is to encourage colleagues to search for additional evidence of parabiosis among basal attines, in order to further corroborate the observation reported and to test the hypotheses proposed here, providing highly relevant contributions for the knowledge on the biology of the Attini, and on the evolution of interspecific relationships.

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