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Research article

Nesting biology of the fungus growing ants *Mycetarotes* Emery (Attini, Formicidae)

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Summary. Fungus-growing ants of the genus *Mycetarotes* are among the least studied in the tribe Attini. This report documents nest architecture and worker population numbers for 19 nests of *M. parallelus* and 5 nests of *M. acutus*, including the first such report for *M. acutus*. This new information is integrated with the scant biological information reported on *Mycetarotes* to date. The resulting picture of *Mycetarotes* life history, as well as the relative ease with which large numbers of nests can be collected and observed in the field, suggest that *Mycetarotes* (particularly *M. parallelus*) is an ideal model system for the study of coevolution of lower-attine ants and their cultivated fungi.

Key words: Mycetarotes, nesting biology, colony size, Attini, fungus-growing ants.

Introduction

Ants of the genus *Mycetarotes* Emery belong to the tribe Attini (Formicidae: Myrmicinae), a monophyletic group of exclusively New World ants (Hölldobler and Wilson, 1990). All known attine species engage in a mutualistic symbiosis with fungi, which they cultivate and use for food. The genus *Mycetarotes* consists of four described species, *M. acutus* Mayhé-Nunes, *M. carinatus* Mayhé-Nunes, *M. parallelus* Emery, and *M. senticosus* Kempf, two of which were only recently recognized (Mayhé-Nunes, 1995). Like a number of other primitive attine genera referred to as 'lower attine' ants (Weber 1982; Wetterer et al., 1998), the genus *Mycetarotes* has been neglected by biologists; we are aware of only four previous publications that have included any information on nesting biology or natural history of this genus (Leuderwaldt, 1918; Kempf, 1960; Mayhé-Nunes, 1995; Leal and Oliveira, 2000). This neglect contrasts sharply with the attention given to the lower attines in the *Cyphomyrmex longiscapus* species group, which has recently become a model system for studying ant-fungus coevolution in Central America (Mueller and Wcislo, 1998; Adams et al., 2000; Green et al., 2002; Mehdiabadi, 2002; Mueller, 2002; Schultz et al., 2002). A parallel model system for South American lower attines is currently unavailable, but *Mycetarotes* has great potential to become such a system due to its local abundance and relative ease of collection. To encourage future research on *Mycetarotes*, we report here the first detailed studies on nest architecture and colony size of two *Mycetarotes* species and integrate these findings with the scant biological information published on the genus to date.

Materials and methods

Fieldwork was conducted in Amazonian Brazil in August 1992 and February–March 2000, and in northeastern Argentina in March–April 2003. A population of *Mycetarotes parallelus* was studied in Parque Nacional Iguazú ("Iguazú 1" in Table 1) during March 28–31, 2003. Additional *M. parallelus* nests used to isolate the ant cultivar and to induce fruiting-body development (not included in our nest descriptions or database) were collected on the campus of the Universidade Estadual Paulista (Rio Claro, SP, Brazil) in July 1997. Nests were located by searching for nest entrance mounds (Fig. 1A and D) and by following foraging workers returning to the colony. Nest architecture was studied by excavating nests by hand (see Schultz, 1993). A pit was first dug adjacent to the nest entrance, at a distance of about 10–20 cm so as not to destroy the nest; once the pit attained the desired depth (approximately 20–30 cm), the excavation proceeded laterally toward the nest entrance until a chamber was encountered. For each chamber, the following measurements were taken: Chamber Depth (distance from the surface of the ground to the floor of the chamber); Chamber Width (greatest horizontal diameter); and Chamber Height (distance from floor to ceiling of the chamber). Ants and fungi were quickly collected from chambers using forceps and aspirators to maximize the percentage of the worker population sampled. An estimate of the minimum colony size was obtained by counting the number of workers collected. Foraging substrate was determined by examining pieces of fungus garden under a dissecting microscope. Latitude, longitude, and elevation were recorded for most collecting sites using handheld GPS receivers. Voucher specimens were deposited at the National Museum of Natural History (Smithsonian Institution), Washington, D.C. (USA), the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas (Brazil), the Museu de Zoologia da Universidade de São Paulo (Brazil), and the Instituto Miguel Lillo, Universidad Nacional de Tucumán (Argentina). *M. parallelus* cultivar fruiting was induced in the Centro de Estudos de Insetos Socais, Rio Claro, by incubating sub-cultured mycelium on sporulation medium in eight culture flasks at 25 °C for 6 weeks, as described by Hervey et al. (1977).

Results

Mycetarotes parallelus

A total of 19 *M. parallelus* nests were excavated at one site in Amazonian Brazil (São Gabriel) and four sites in northeastern Argentina (Iguazú 1, Iguazú 2, Rhea Farm, and Chaco Park; see Table 1 for full site descriptions and sample sizes per site). The mean number of workers collected was 110.6 (N = 13 nests), which represents a minimum estimate for colony size. A single, dealate queen was collected in 12 of the 19 nests; no nests were found with more than a single queen, suggesting that this species is monogynous. The majority of nests (84%) consisted of a single nest entrance leading to a single chamber, which contained the fungus garden, brood, and queen. However, two nests (TRS030331-02, UGM030406-01) consisted of two chambers each, an upper ("first") and lower ("second") chamber, horizontally offset from one another (average distance between chambers was 1.5 cm). In at least one of these nests (TRS030331-02), the shallow (5 cm), upper chamber was likely to be the foundress chamber where the queen first established her nest. In other lower-attine species, such superficial chambers are typically abandoned as the colony grows and new, deeper chambers are constructed (Weber, 1972; Mueller, pers. obs.; Schultz, pers. obs.). The average first chamber depth, width, and height for all *M. parallelus* nests collected were 10.8 cm (N = 18), 4.9 cm (N = 16), and 4.2 cm (N = 14), respectively. The foraging substrate used to cultivate the fungus garden in these nests (N = 4) consisted primarily of vegetative material, including seeds, buds, leaf fragments, and grass bits; no insect parts were found. Alate queens and males were collected in only one nest (TRS920824-01), at São Gabriel in August 1992. The chamber floor of this nest was covered with a fine granular material, possibly garden waste, and populated by arthropod commensals, including polydesmid millipedes.

A detailed population survey was conducted at Iguazú 1, where fourteen *M. parallelus* nests were collected during March 28–31, 2003. At the time of our observations (autumn), colonies at this site appeared to be in the process of disposing of some of the garden biomass, and exhausted fungal material had accumulated in piles, 1–2 cm high, surrounding the nest entrances (Fig. 1A). While some fungus gardens completely filled the chambers they occupied, many of the gardens were noticeably smaller than their respective chambers. This may be indicative of an annual pattern of garden size reduction during autumn to prepare the colony for winter, which is typical for other subtropical and temperate attines (Weber, 1972; Mueller, pers. obs.). Fungus gardens were consistently suspended from rootlets emerging from the chamber roof (Fig. 1B). Queens, collected in 10 of the 14 nests at Iquazú 1, were usually found hiding within the garden. The gardens contained many pupae, covered with mycelial coats (common among attine species; Weber, 1972; Schultz and Meier, 1995), but few larvae and no alates were collected at Iguazú 1; this too is consistent with the hypothesis suggested above that the colonies were preparing for a period of overwintering.

After 5 weeks of cultivation in sporulation medium, *M. parallelus* cultivar began to develop fruiting bodies, which matured in four to six days. Fruiting structures were produced in six of eight culture flasks; in the other two flasks the fungus remained in a vegetative state typical for laboratory cultures. Three to six fruiting-bodies were simultaneously produced in each of the culture flasks, one of which is shown in Figure 2.

Mycetarotes acutus

Five *M. acutus* nests were excavated at three different forested sites (Reserva Ducke, Camp 41, Dimona Camp) near Manaus, Amazonas, Brazil, in August 1992, as well as February and August 2000. The nests had a single entrance turret made from excavated sand or clay pellets (Fig. 1D); the average turret height was 2.3 cm and average width was 1.3 cm (N = 4). The worker population was estimated to be 20–30 workers based on observations from one nest. Each nest had a single chamber, an average of 11.6 cm below ground. The average chamber width was 5.1 cm (N = 5) and average chamber height was 5.0 cm (N = 3) (Table 1). The fungus garden was typically found suspended from rootlets hanging within the chamber. The foraging substrate consisted primarily of seeds, flower stamens, and unidentified plant fibers. One nest (UGM000228-01) contained a disc-shaped, tar-like wad (1.5 cm × 2 cm × 5 mm high) of compacted, discarded fungal material in the corner of the garden chamber.

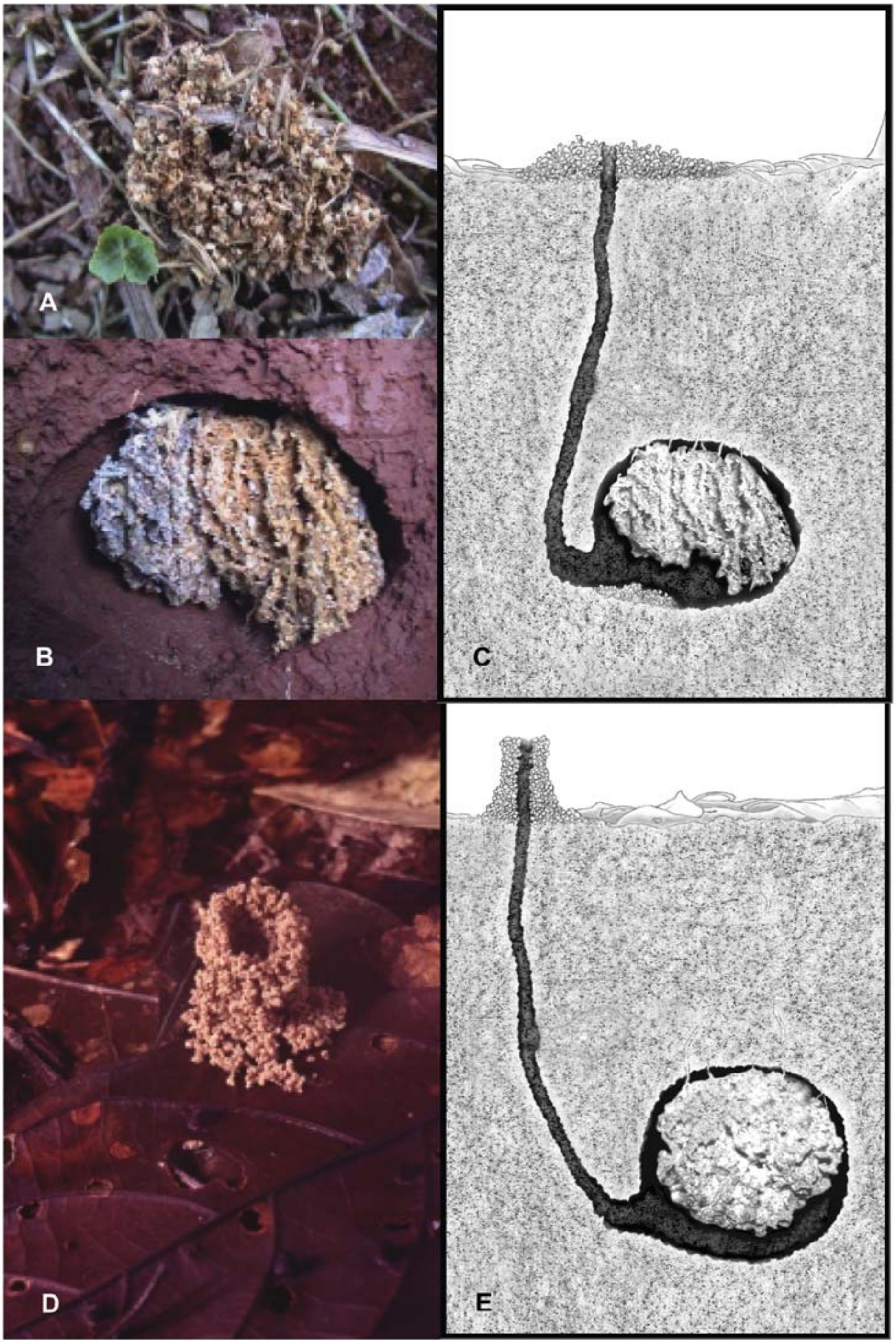

Figure 1. Nests of *Mycetarotes* species. A–C: *M. parallelus*; D–E: *M. acutus*. (A) *M. parallelus* nest entrance ringed by exhausted fungal substrate, with entrance hole visible in middle; (B) Cross-section of *M. parallelus* garden chamber, where fresh fungal garden (gray-green) can be distinguished from older fungal garden (yellow-brown). The garden is suspended from rootlets emerging from the top of the chamber. The chamber width and height are 7.3 cm and 5.4 cm, respectively; (C) Schematic drawing of cross-section through a nest of *M. parallelus*; (D) *M. acutus* nest entrance. The turret is made of clay and emerges 3 cm above a thin layer of leaves on the forest floor; (E) Schematic diagram showing a cross-section through a *M. acutus* nest. Photos by U. Mueller; drawings by B. Klein

Discussion

Combining our data with what is currently known of the genus *Mycetarotes* (see Table 2), we can begin to draw some conclusions about the natural history of one of the least-understood genera of attine ants. Information on nest architecture is now known for three of the four species (*M. parallelus, M. carinatus,* and *M. acutus*), and nests are similar between the species. Indeed, based on our data there are no significant differences between the average chamber depths, widths, or heights for the two species examined in this study. The subterranean nest architecture in this genus is similar to that of other lower attines, such as *Mycocepurus*, *Mycetosoritis*, and *Mycetophylax* (Wheeler, 1907; Weber, 1972; Mueller, pers. obs.), except that many species in these other genera construct multiple chambers in a vertical series of deeper and deeper chambers, whereas *Mycetarotes* constructs, with few exceptions, only a single subterranean chamber.

Table 1. Summary of *Mycetarotes* spp. nests collected between August 1992 and April 2003[1]

Colony ID	Species	No. of Chambers	First Chamber			Second Chamber			Workers Collected	Queens Collected	Site Name, Country
			C D	C W	C H	C D	C W	C H			
SES030331-01	*parallelus*	1	10.0	3.0	4.0	–	–	–	52	1	Iguazú 1, Argentina
SES030331-02	*parallelus*	1	12.0	2.0	2.5	–	–	–	5	0	Iguazú 1, Argentina
SES030331-03	*parallelus*	1	12.0	5.0	5.0	–	–	–	130	1	Iguazú 1, Argentina
SES030331-04	*parallelus*	1	11.0	4.0	4.0	–	–	–	95	0	Iguazú 1, Argentina
SES030331-05	*parallelus*	1	9.0	7.0	5.0	–	–	–	?	?	Iguazú 1, Argentina
TRS030331-02	*parallelus*	2	5.0	?	?	10.0	2.0	2.0	46	1	Iguazú 1, Argentina
TRS030328-01	*parallelus*	1	8.0	2.5	2.0	–	–	–	?	?	Iguazú 1, Argentina
UGM030328-01	*parallelus*	1	14.5	5.7	8.2	–	–	–	162	1	Iguazú 1, Argentina
UGM030328-02	*parallelus*	1	13.5	10.4	5.6	–	–	–	136	1	Iguazú 1, Argentina
UGM030331-01	*parallelus*	1	13.5	2.6	2.9	–	–	–	19	1	Iguazú 1, Argentina
UGM030331-02	*parallelus*	1	14.0	7.3	5.4	–	–	–	258	1	Iguazú 1, Argentina
UGM030331-04	*parallelus*	1	13.0	5.6	5.0	–	–	–	225	1	Iguazú 1, Argentina
CC030328-02	*parallelus*	1	9.0	4.0	?	–	–	–	?	1	Iguazú 1, Argentina
CC030328-03	*parallelus*	1	12.0	3.5	?	–	–	–	?	1	Iguazú 1, Argentina
SP030329-01	*parallelus*	1	6.0	?	?	–	–	–	?	?	Iguazú 2, Argentina
UGM030405-01	*parallelus*	1	9.7	4.6	3.4	–	–	–	131	1	Rhea Farm, Argentina
CC030405-01	*parallelus*	1	?	?	?	–	–	–	119	0	Rhea Farm, Argentina
UGM030406-01	*parallelus*	2	11.0	3.8	2.2	14.5	2.2	2.1	60	1	Chaco Park, Argentina
TRS920824-01	*parallelus*	1	12.0	7.0	4.0	–	–	–	?	?	São Gabriel, Brazil
Mean			10.8	4.9	4.2	12.3	2.1	2.1	111		
Standard Dev.			3.9	2.0	3.2	6.1	0.1	79.9	76		
N			18	16	14	2	2	2	13		
TRS920807-11	*acutus*	1	8.0	5.0	?	–	–	–	?	1	Reserva Ducke, Brazil
TRS920807-12	*acutus*	1	3.0	5.0	7.0	–	–	–	?	?	Reserva Ducke, Brazil
TRS000227-06	*acutus*	1	18.0	7.0	5.0	–	–	–	?	?	Camp 41, Brazil
UGM000228-01	*acutus*	1	16.0	4.5	?	–	–	–	?	?	Camp 41, Brazil
TRS 000819-01	*acutus*	1	13.0	4.0	3.0	–	–	–	?	1	Dimona Camp, Brazil
Mean			11.6	5.1	5.0	–	–	–	–		
Standard Dev.			6.1	1.1	2.0	–	–	–	–		
N			5	5	3	0	0	0	0		

[1] CD = Chamber depth in cm; CW = Chamber width in cm; CH = Chamber height in cm.
"–" indicates data not applicable; "?" indicates data not taken; Iguazú 1 = Gendarmeria Nacional Station, Parque Nacional Iguazú, Provincia de Misiones, 25° 42.815′S, 54° 27.701′W; Iguazú 2 = Casa de los Guardaparques, Parque Nacional Iguazú, Provincia de Misiones, Argentina, 25° 42.888′S, 54° 26.450′W; Rhea Farm = km 61 on Ruta 16, Provincia de Chaco, Argentina, 27° 10.946′S, 59° 19.852′W; Chaco Park = Campground at Parque Nacional Chaco, Provincia de Chaco, Argentina, 26° 48.522′S, 59° 36.395′W; São Gabriel = São Gabriel de Cachoeira, Serra Boa Esperanza, Amazonas, Brazil, no GPS data available; Reserva Ducke = Reserva Ducke, Manaus, Amazonas, Brazil, 2° 56.315′S, 59° 57.768′W; Camp 41 = BDFFP Camp 41, Manaus, Amazonas, Brazil, 2° 26.948′S, 59° 46.199′W; Dimona Camp = BDFFP Dimona Camp, Manaus, Amazonas, Brazil, 2° 20.347′S, 60° 5.71′W

This is the first study to estimate the number of workers in *Mycetarotes* nests based on actual excavations. The average number of workers in *M. parallelus* was 111. This is lower than the average lower-attine colony size of approximately 350 workers (Price et al., 2003), but is consistent with the traditional assumption that more primitive attine species have smaller colony sizes (Schultz and Meier, 1995). This is also the first published description of the nest of *M. acutus*, which was previously known only from a single stray worker collected by E. F. Morato in 1990 and deposited in the Museu de Zoologia da Universidade de São Paulo (São Paulo, SP, Brazil).

The genus *Cyphomyrmex* has recently become a model system for Central American lower attines (Mueller and Wcislo, 1998; Schultz et al., 2002), and has been used to investigate the prevalence of, and mechanism for, the exchange of fungal cultivars between attine species (Adams et al., 2000; Green et al., 2002; Mehdiabadi, 2002; Mueller et al., 2004). A parallel system for South American lower attines is currently lacking, but development of such a system could facilitate attine research for two principle reasons. First, attine diversity is highest in South America (Weber, 1972; Hölldobler and Wilson, 1990), and thus a model attine system representing this geographical region would be most informative. Second, the attine ant-fungus symbiosis is thought to have originated in South America (Mueller et al., 2001); investigations into the origin of this symbiosis should therefore focus on ants and fungi from this region.

We believe that *Mycetarotes* could become the South American lower attine model system for five reasons. First,

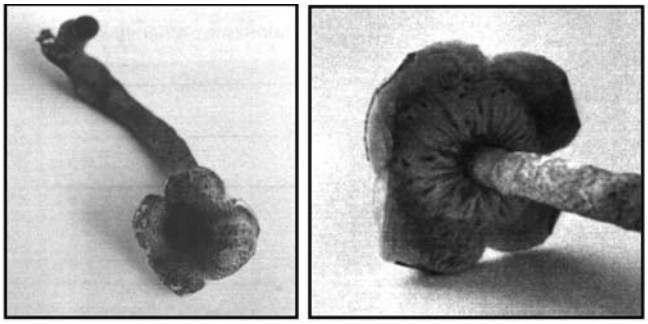

Figure 2. Fruiting-body of *M. parallelus* cultivar. Nests of *M. parallelus* were collected on the campus of the Universidade Estadual Paulista in Rio Claro, SP, Brazil. Fruiting-body formation was observed in six of eight replicates after six weeks of cultivation on sporulation medium (Photos by M. Bacci).

we found nests of *M. parallelus* to be locally abundant (e.g. at Iguazú 1 and Iguazú 2), and excavating nests proved to be simple; the chambers, each containing a single fungus garden, the queen, and the brood, were only 5–18 cm below ground. Large numbers of queenright nests can therefore be collected in a short time. This is a significant advantage over other lower attines, such as *Mycocepurus*, which may be more locally abundant but which require significantly more effort to collect complete nests due to the depths at which the multiple fungus chambers occur. Second, *Mycetarotes* colonies can be maintained for several years in the laboratory (see set-up described in Schultz 1993) for use in behavioral observations and other experiments. Third, *Mycetarotes*, unlike *Cyphomyrmex*, is one of the more basal genera of lower-attines (Schultz and Meier, 1995), and is therefore more likely to have retained characters present in the common ancestor of the tribe Attini. Fourth, the fungi cultivated by *M. parallelus* and *M. acutus* were included in a phylogenetic analysis of lower attine fungi (Mueller et al., 1998;

Table 2. Summary of natural history information to date on all species of *Mycetarotes*, integrating data from this study with previously published reports.

	M. parallelus	*M. acutus*	*M. carinatus*	*M. senticosus*
Geographical Distribution[1]	Brazil: AM, GO, MG, RJ, SP; Argentina: CH, MS, TU	Brazil: AM	Brazil: RJ	Brazil: RJ, SC, SP
Habitat	Open fields, disturbed habitats, secondary forest, gallery forest	Forest	Clearing in secondary forest	?
# Nests Excavated	23	5	1	0
Nest Entrance Description	Mound (1–4 cm high) or dump (1–2 cm high)	Turret (1–3 cm high)	Hole (3 mm diameter)	?
# Chambers	1 or 2	1	1	?
Chamber Depth	5.0–14.5 cm (~11 cm mean)[2]	3.0–18.0 cm (11.6 mean)	13 cm	?
Chamber Width	2.0–10.4 cm (~5 cm mean)[2]	4.0–7.0 cm (5.1 mean)	7 cm	?
Chamber Height	2.0–8.2 cm (~4.2 mean)[2]	3.0–7.0 cm (5.0 mean)	4 cm	?
# Workers	5–258 (111 mean)	20–30	?	?
Garden Description	Suspended from rootlets	Suspended from rootlets or resting on floor	Suspended from rootlets	?
Foraging Substrate	Seeds, buds, leaf and grass fragments	?	?	?
Notes	Fungal basidiocarp observed to develop from pure cultivar isolate in lab	–	–	–
References	Luederwaldt, 1918; Kempf, 1960; Mayhé-Nunes, 1995; Leal and Oliveira, 2000; Mueller, 2002	Mayhé-Nunes, 1995	Mayhé-Nunes, 1995	Kempf, 1960

[1] BRAZIL: AM = Amazonas, GO = Goias, MG = Minas Gerais, RJ = Rio de Janeiro, SC = Santa Catarina, SP = São Paulo; ARGENTINA: CH = Chaco, MS = Misiones, TU = Tucumán.
[2] The exact mean cannot be calculated because only a range is given in Mayhé-Nunes (1995).

M. acutus was incorrectly identified as *M. senticosus* in this analysis); each of these *Mycetarotes* species cultivates fungal cultivars in different cultivar clades (Fig. 1 in Mueller et al., 1998), suggesting that speciation in *Mycetarotes* may be coincident with switches to novel cultivars, as has been suspected for other lower attines (Mueller, 2002; Schultz et al., 2002). Fifth, the cultivar of *M. parallelus* has been shown to be capable of fruiting-body development (Fig. 2; Oliveira da Silva-Pinhati et al., in prep.), indicating that this cultivar may have close links to free-living, nonsymbiotic fungal populations. We therefore suggest that *Mycetarotes*, particularly *M. parallelus*, could be used as a model system for studying the ecological and evolutionary relationships between lower attine ants and their fungi, and, as such, has the potential to significantly advance our understanding of the symbiosis between lower attine ants and their fungal cultivars.

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