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Research article

Foraging ecology of attine ants in a Neotropical savanna: seasonal use of fungal substrate in the cerrado vegetation of Brazil

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Summary. In this study we identified the material collected as fungal substrate by attine ants in the cerrado vegetation of Southeast Brazil. A total of 313 colonies of the evolutionary more primitive (genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*) and transitional attines (genera *Sericomyrmex* and *Trachymyrmex*) were marked in the field and monitored monthly, during one year. Attines collected material from 53 plant species in 28 families. Items included leaves, flowers, fruits, seeds, wood, mosses, lichens, insect feces and corpses. Flowers and fruits were the items most frequently collected by all genera, especially during the wet season when these plant parts are more abundant in the cerrado. During the dry season, the ants diversified the material collected, and the frequency of different items varied across the ant genera. The most primitive genera collected mainly insect feces and corpses, while the intermediate ones relied on vegetative plant parts such as recently fallen leaflets. Seeds and other materials such as mosses, lichens, and wood were also more commonly used during dry months. The use of these resources was associated with greater foraging distances by all genera in dry months. The results indicate that lower attines present an opportunistic foraging behavior, by collecting items in the vicinity of their nests, and in accordance with the phenology of the cerrado vegetation. We briefly discuss some general evolutionary trends within the Attini.

Key words: Ant-plant interaction, Attini, cerrado vegetation, foraging behavior.

Introduction

The ant tribe Attini (Myrmicinae) comprises 12 genera and 202 species distributed throughout the Neartic and Neotropical regions between latitudes of approximately 40°N and 40°S (Weber, 1972). These ants maintain an obligate mutualism with symbiotic fungi, which are cultured inside the nest on a plant-derived substrate collected by the ants (Hölldobler and Wilson, 1990). The cultured fungus is the only food source for the larvae and probably constitutes the principal food item of the so-called lower attines (Stradling, 1991).

Because of the leaf-cutting behavior of the more advanced genera *Atta* and *Acromyrmex,* attine ants have been considered to be among the most serious agricultural insect pests, mainly in the Neotropical region (Cherrett, 1986; Wilson, 1986; Vander Meer et al., 1990). Notwithstanding, the material collected by lower attines for the fungus garden is poorly known (Garling, 1979; Stradling, 1991). Myrmecologists have generally considered insect remains and decaying plant matter as the main substrate used by lower attines (Weber, 1941; 1945; 1946; 1957; Wilson, 1971; Garling, 1979; Hölldobler and Wilson, 1990; Mayhé-Nunes, 1995). A review of the literature, however, revealed that these ants may collect fresh plant parts. For instance, *Sericomyrmex* and *Trachymyrmex* collect leaves (Weber, 1972; Mayhé-Nunes, 1995). Flowers are reported as fungal substrate for *Mycetosoritis hartmanni* (Wheeler, 1907), and for species of *Mycocepurus* and *Trachymyrmex* (Wheeler, 1907; Kempf, 1963). Fruit pulp is collected by *Mycocepurus goeldi* (Oliveira et al., 1995), as well as by *Cyphomyrmex*, *Sericomyrmex* and *Trachymyrmex* species (Pizo and Oliveira, 2000). Finally, seeds are gathered by *Cyphomyrmex faunulus* (Weber, 1946), *Mycetarotes parallellus*, *Mycocepurus smithi* (Weber, 1945; Mayhé-Nunes, 1995), and *Apterostigma*, *Cyphomyrmex*, *Sericomyrmex* and *Trachymyrmex* species (Kaspari, 1993; Pizo and Oliveira, 1999, 2000). Nonetheless, most of these studies are based on opportunistic rather than systematic surveys of the fungus substrate collected by these ants.

Using traits such as worker morphology, nest structure and colony size, as well as fungal substrate, Hölldobler and Wilson (1990) summarized data from previous studies and

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roughly subdivided the attine genera into three categories, primitive (*Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Apterostigma*), transitional (*Sericomyrmex*, *Mycetosoritis*, and *Trachymyrmex*) and advanced (*Atta* and *Acromyrmex*). Although a good amount of ecological data is available for the more advanced genera, very little is known on the natural history and ecology of the transitional and primitive taxa. In this paper we intend to fill this gap by identifying the material utilized for fungus-culturing by each of six genera of the so-called lower attines (*Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*) in the cerrado vegetation of Brazil. We systematically recorded the seasonal variation in the composition of items collected by workers, as well as the foraging distances relative to their nests. We used these data to revise and briefly discuss current evolutionary trends proposed for the Attini.

Materials and methods

Field work was carried out in the cerrado reserve of the Estação Experimental de Mogi-Guaçu (22°18′S, 47°13′W), São Paulo, Southeast Brazil. The Brazilian cerrados embrace an area of 2 million km^2, and within their distribution they present several intergrading physiognomic forms ranging from open grassland with scattered shrubs to forest (Goodland, 1971; Gottsberger and Silberbauer-Gottsberger, 1983). Gibbs et al. (1983) give a detailed floristic analysis of the cerrado of Mogi-Guaçu, and Mantovani and Martins (1988) provide a phenological account of the vegetation of this area. The climate of the region is characterized by a dry/cold period from April to September and a wet/warm season from October to March. Mean monthly temperature ranges from 8.7 °C in July to 30.4 °C in February, and maximum monthly rainfall is 235 mm in December (De Vuono et al., 1986).

During March and April 1995 we selected five trails (totalling 7 km) in the cerrado *sensu stricto* (see Goodland, 1971), as well as in the transition between the open cerrado and gallery forest. Baits made of fruits (orange) and dry oats were used to attract attine ants and locate their nests along the trails. We marked nests of *Cyphomyrmex* (N = 22), *Mycetarotes* (N = 8), *Mycocepurus* (N = 197), *Myrmicocrypta* (N = 41), *Sericomyrmex* (N = 6) and *Trachymyrmex* (N = 39). Seasonal variation of foraging activity in all nests was monitored monthly, from May 1995 to April 1996. We recorded ant activity in each marked nest during a 5 min session, between 08.00 and 18.00 h. With the exception of *Cyphomyrmex* which was active both day and night, all other genera presented only diurnal activity (Leal, 1998). The material collected by workers for fungus-culturing and its distance from the nest were registered during such censuses. Data are expressed as the number of occasions in which a given colony was seen collecting a particular item for fungus-culturing. Voucher specimens of Attini species are deposited at the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil. A detailed account of the interactions between attines, fruits and seeds in the cerrado is given by Leal and Oliveira (1998).

Results

The 313 marked colonies were distributed in 6 genera and 19 morpho-species, as shown in Table 1. *Mycocepurus* was the most abundant genus (197 marked colonies) and *Trachymyrmex* the most diverse (10 species). In general, the distribution patterns of attine species were related to the vegetation type of the study area. While *Mycetarotes parallellus* was always observed nesting in the gallery forest, *Cyphomyrmex*, *Mycocepurus*, *Myrmicocrypta* and *Sericomyrmex* species were more abundant in the cerrado areas. On the other hand, species of *Trachymyrmex* were more commonly recorded in open and dry sites. As a rule the attine fauna was more abundant and diverse in cerrado habitats than in forested areas (see Table 1).

Table 1. Attine species and number of colonies marked in three different vegetation types of the Mogi-Guaçu Reserve, Southeast Brazil

Species	Number of marked colonies		
	Cerrado *sensu stricto* [a]	Open cerrado [b]	Gallery Forest
Cyphomyrmex gr. *rimosus* sp. 1	3	–	–
Cyphomyrmex gr. *rimosus* sp. 2	7	1	3
Cyphomyrmex gr. *strigatus* sp. 1	5	–	1
Cyphomyrmex gr. *strigatus* sp. 2	2	–	–
Mycetarotes parallellus (Emery)	–	–	8
Mycocepurus goeldi Forel	137	42	16
Mycocepurus sp. n.	2	–	–
Myrmicocrypta sp.	30	10	1
Sericomyrmex sp.	6	–	–
Trachymyrmex dichrous Kempf	3	–	–
Trachymyrmex fuscus Emery	–	3	–
Trachymyrmex sp. 1	–	2	–
Trachymyrmex sp. 2	–	1	–
Trachymyrmex sp. 3	–	2	–
Trachymyrmex sp. 4	5	10	2
Trachymyrmex sp. 5	–	1	–
Trachymyrmex sp. 6	1	2	–
Trachymyrmex sp. 7	3	3	–
Trachymyrmex sp. 8	–	1	–
Total of colonies	204	78	31
Total of species	12	12	6

[a] Dense scrub of shrubs and trees.
[b] Scattered shrubs with dense herbaceous layer, also known as "campo-cerrado" (see Goodland, 1971).

A total of 53 plant species from 28 families were collected by attine ants (Table 2). The Compositae, Graminae, Leguminosae, Melastomataceae and Rubiaceae were the most important plant families for the ants, both in number of species collected and in number of records. Items included leaves, flowers, fruits, seeds, wood, mosses, lichens, insect feces and corpses (Table 2). Flowers and fruits were the items most frequently used by the ants, especially during the wet season. During the dry months the ants diversified the material collected, and included increased quantities of leaves, seeds, insect feces, and other material such as mosses, lichens, wood and insect corpses (Fig. 1). Soft plant parts such as flowers and fruits were usually transported as entire units, and only occasionally were they cut into pieces. On the other hand, there were no records of attines cutting tough plant parts such as leaves and seeds. Soft vegetative plant parts consisted of fallen leaflets of *Anadenanthera falcata* (> 95% of records, Leguminosae, Mim.), and small leaves of *Phyllanthus niruri* (< 5% of records, Euphorbiaceae) (Table 2). Seeds were collected beneath the plant canopies or

Table 2. Material collected by attine ants for fungus-culturing in the cerrado of Mogi-Guaçu, Southeast Brazil. Values refer to number of records (i.e., occasions in which a colony was seen collecting a particular item)

Plant family	Plant species	Plant parts			
		Leaves	Flowers	Fruits	Seeds
Annonaceae	*Xylopia aromatica* Baill	–	13	–	2
Apocynaceae	*Aspidosperma tomentosum* Mart	–	7	–	–
Araliaceae	*Didymopanax vinosum* March.	–	21	15	–
Bignoniaceae	*Pyrostegia venusta* Miers	–	10	–	–
Boraginaceae	*Cordia sellowiana* Cham.	–	11	12	–
Clusiaceae	*Kielmeyera rubriflora* Camb.	–	2	–	–
Compositae	*Eupatorium* sp.	–	6	–	–
	Gochnatia barrosii Cabrera	–	7	–	–
	Gochnatia pulcra Cabrera	–	28	–	–
	Vernonea scorpioides Pers.	–	15	–	–
Cyperaceae	*Bulbostyles* cf. *capillaris* Nees	–	19	–	–
Euphorbiaceae	*Pera obovata* Baill.	–	2	–	14
	Phyllanthus niruri Thunb.	5	5	–	–
Gramineae	*Axonopus barbigerus* Hitchcock	–	37	–	–
	Echinolaena inflexa Chase	–	34	–	–
	Ichnanthus inconstans Doell	–	10	–	–
	Mellinis minutiflora Beauv.	–	15	–	–
Lauraceae	*Ocotea pulchella* Mart.	–	19	36	–
Leguminosae-Caes.	*Copaifera langsdorfii* Desf.	–	3	–	48
	Hymenaea courbaril Linn.	–	3	7	–
Leguminosae-Mim.	*Anadenanthera falcata* Speg.	111	–	–	8
Leguminosae-Pap.	*Bowdichia virgilioides* H.B. & K.	–	7	–	–
Malpighiaceae	*Banisteriopsis* sp.	–	9	–	–
	Byrsonima intermedia A. Juss.	–	34	7	–
	Byrsonima verbascifolia Rich. ex Juss.	–	19	–	–
Melastomataceae	*Miconia albicans* Steud.	–	14	17	4
	Miconia estenostachya DC.	–	4	–	–
	Miconia fallax DC.	–	4	–	–
	Miconia ligustroides Naud.	–	8	12	–
	Miconia pohliana Cogn.	–	3	–	–
	Miconia rubiginosa DC.	–	12	13	3
Meliaceae	*Trichilia pallida* Sw.	–	5	13	3
Monimiaceae	*Siparuna guianensis* Aubl.	–	–	–	3
Moraceae	*Ficus citrifolia* Mill	–	–	2	–
Myristicaceae	*Virola sebifera* Aubl.	–	8	–	2
Myrsinaceae	*Rapanea ferruginea* Mez.	–	6	1	–
	Rapanea umbellata Mez.	–	22	75	5
Myrtaceae	*Eugenia* cf. *pitanga* Arech.	–	5	–	–
Ochnaceae	*Ouratea spectabilis* Engl.	–	15	27	–
Palmae	*Syagrus flexuosa* Becc.	–	3	–	–
Rosaceae	*Prunus sellowii*	–	–	36	–
Rubiaceae	*Borreria* sp.	–	7	–	–
	Diodia sp.	–	3	–	–
	Hemidiodia sp.	–	2	–	–
	Palicourea rigida H.B. & K.	–	–	–	6
	Psychotria barbiflora DC.	–	–	–	2
	Psychotria stachyoides Benth.	–	–	3	12
	Rudgea viburnoides Benth.	–	–	6	2
Rutaceae	*Zanthoxylum rhoifolium* Lam.	–	–	4	–
Sapindaceae	*Serjania lethalis* A. St. Hil.	–	43	–	–
Solanaceae	*Solanum* sp.	–	–	–	4
Styracaceae	*Styrax ferrugineus* Ness & Mart.	–	8	–	–
Vochysiaceae	*Qualea grandiflora* Mart.	–	1	5	–
	Vochysia tucanorum Mart.	–	13	–	–

Other types of material	*Number of records*
Mosses	6
Lichens	4
Wood	24
Unidentified plant material	29
Insect feces	103
Insect corpses	43

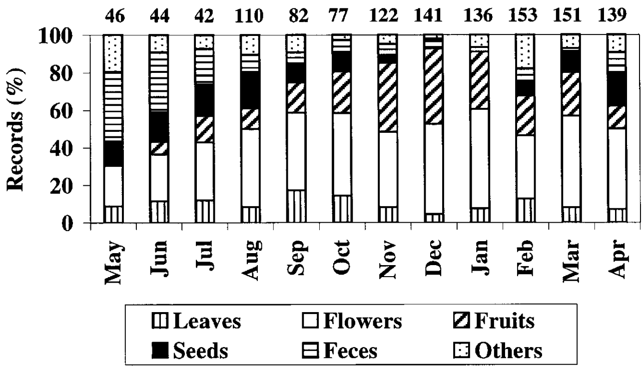

Figure 1. Items collected by tribe Attini during 12 months in the cerrado of Mogi-Guaçu, Southeast Brazil. Values above bars refer to number of records per month

from vertebrate feces. We observed *Mycocepurus goeldi* and *Trachymyrmex* species using seed endosperm of *Copaifera langsdorfii* (Leguminosae, Caes.) and *Didymopanax vinosum* (Araliaceae) after seed scarification by *Atta sexdens*. For more details on the interaction between attines (including *Acromyrmex* and *Atta*) and fruits and seeds in the cerrado, see Leal and Oliveira (1998).

The preference for soft plant parts becomes evident as we consider the attine genera separately (Fig. 2A–F). Ants collected flowers or fruits whenever these resources were found close to their nests. However, as these items become rare during the dry season, ants from different genera may switch to different substrates. Seeds, insect feces (especially from defoliating caterpillars and wood-boring beetles), and corpses were harvested more commonly by species of the more primitive genera, *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus* and *Myrmicocrypta* (Fig. 2A–D). Conversely, the utilization of leaves was more pronounced in the evolutionary intermediate genera, *Sericomyrmex* and *Trachymyrmex* (Fig. 2E, F).

Foraging by attine species always took place on the ground in close vicinity of their nests (5–700 cm, N = 1123 records, Table 3). Consequently, the availability of potential resources varied with the location of nesting sites. For example *Mycocepurus* ants, which may nest in different habitats (Table 1), collected a higher diversity of items than other genera. On the other hand, the substrate used by *Trachymyrmex* species consisted mostly of grasses, which comprise the main plant component of the open cerrado (see Table 1). Foraging distances of all genera were significantly greater in the dry season than during the wet season; *Sericomyrmex* and *Trachymyrmex* foraged slightly longer distances than the other genera (Table 3).

Discussion

The current study is the first to provide a seasonal quantitative account of the diversity of items collected by primitive

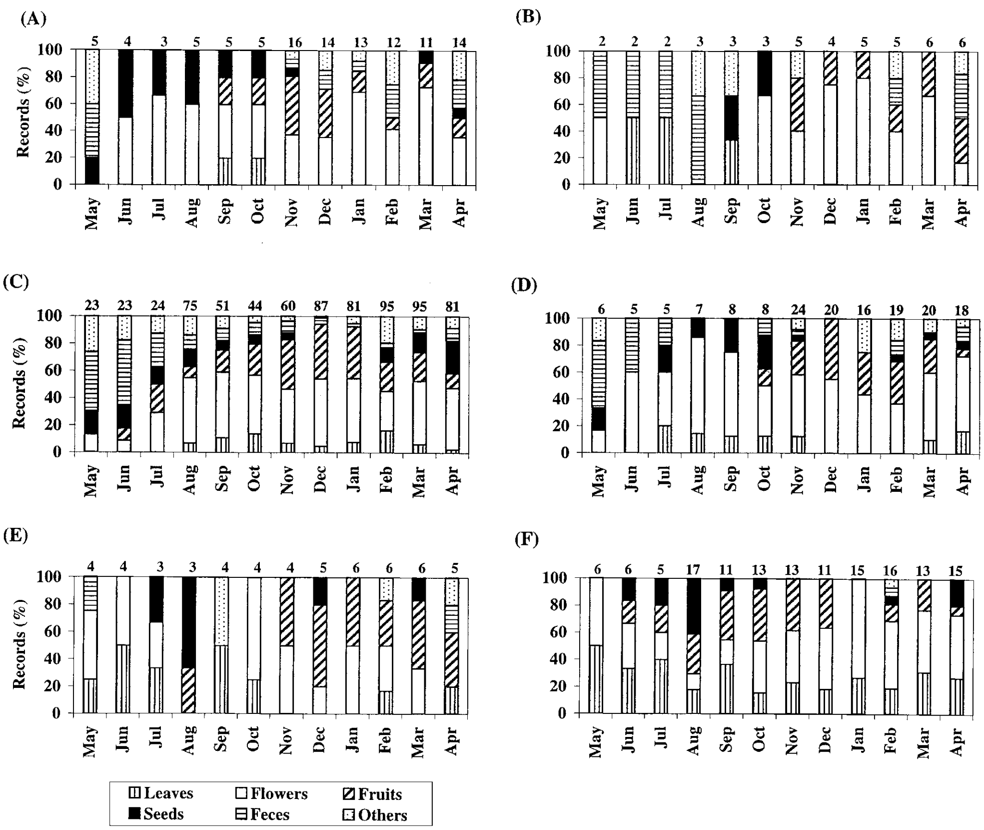

Figure 2. Items collected by Attini genera during 12 months in the cerrado of Mogi-Guaçu, Southeast Brazil. **A)** *Cyphomyrmex*, **B)** *Mycetarotes*, **C)** *Mycocepurus*, **D)** *Myrmicocrypta*, **E)** *Sericomyrmex* and **F)** *Trachymyrmex*. Values above bars refer to number of records per month

Table 3. Foraging distances of attine ant genera in the cerrado of Mogi-Guaçu, Southeast Brazil. Values are means ± SD. The number of observations is given in parentheses

Genera	Total	Foraging distance (cm)		
		Dry season	Wet season	P (*t* test)
Tribe Attini	137.02 ± 107.06 (1123)	172.43 ± 123.71 (404)	117.12 ± 90.65 (719)	0.0000
Cyphomyrmex	124.65 ± 104.43 (93)	167.10 ± 134.58 (29)	105.41 ± 81.66 (64)	0.0076
Mycetarotes	127.43 ± 101.76 (42)	176.65 ± 105.48 (17)	93.96 ± 85.95 (25)	0.0118
Mycocepurus	129.00 ± 98.12 (668)	157.79 ± 114.09 (238)	113.07 ± 84.05 (430)	0.0000
Myrmicocrypta	120.32 ± 83.97 (158)	146.92 ± 102.63 (50)	108.01 ± 70.98 (108)	0.0064
Sericomyrmex	149.02 ± 107.00 (33)	203.33 ± 107.70 (19)	88.50 ± 70.23 (14)	0.0199
Trachymyrmex	217.02 ± 149.66 (129)	264.82 ± 154.91 (51)	182.19 ± 136.54 (70)	0.0031

and intermediate attines for fungus-culturing in cerrado vegetation. The results revealed that these ants are very opportunistic and utilize plant parts according to the phenology of the vegetation (as in Mantovani and Martins, 1988). These attines prefer to collect available items from nearby plants. The statement that insect remains and decaying plant matter are the main substrates used by lower attines (Weber, 1941; 1945; 1946 and 1957; Garling, 1979; Wilson, 1971; Hölldobler and Wilson, 1990; Mayhé-Nunes, 1995) needs revision. Recently-fallen flowers and fruits comprised the major part of the fungus-substrate used by all genera studied here. Tougher plant parts, such as leaves and seeds, insect remains, and other material also were used by the ants, particularly in the dry season, probably to compensate for the lower availability of flowers and fruits during this period.

During this study the ants always harvested the fungal substrate on the ground. This observation agrees with the reviews of *Mycocepurus* and *Cyphomyrmex* (Kempf, 1963; 1964; 1965), where he stated that these ants never climb on plants to cut the fungus substrate. Nevertheless, we frequently observed a *Trachymyrmex* species climbing on *Tibouchina stenocarpa* (Melastomataceae) to cut flowers, during a one-month study in an area of cerrado close to Mogi-Guaçu (data not shown). Since *Acromyrmex* and *Atta* frequently climb on the vegetation to cut the fungus substrate, we believe that this behavior is rare for the primitive genera, but becomes more common in the more evolutionary advanced genera of the tribe Attini.

Mean foraging distances of lower attines was 1 to 2 m, which is considerably shorter than that recorded for the leaf-cutters *Acromyrmex* and *Atta*, which may reach tens, or even hundreds of meters (Cherrett, 1968; Lewis et al., 1974a; b). Apparently, due to their small colony and worker size, lower attines cover a smaller area than *Acromyrmex* and *Atta*. A positive relationship between colony size and foraging distance has been detected for *Atta cephalotes* (Lewis et al., 1974a) and *A. sexdens* (Fowler and Robinson, 1979). In small colonies of *A. cephalotes*, Wetterer (1994) found that small-sized foragers cut herbs within 7 m from the nest, whereas larger colonies recruited a broader size-range of workers to distances up to 80 m from the nest. Based on our data we suggest that there is a trend of increased foraging distances with genera derivation, probably due to the trends of increased colony and worker size (Wilson, 1971; Hölldobler and Wilson, 1990). Stradling and Powell (1986) have suggested that differential productivity among fungal strains was a major factor in the speciation of the attines, with a more productive crop permitting a large worker population and an increased foraging range in the more advanced groups.

Since vegetation phenology and thus resource availability is related to physical factors (Opler et al., 1976), we would expect a strong effect of seasonality on the foraging pattern of attines in the cerrado. During dry months plant biomass is significantly reduced in the cerrado due to drought, decreased temperature and photoperiod, as well as fire (Mantovani and Martins, 1988). We recorded maximum foraging distances during the dry season for all attines studied. This is probably due to the lower availability of flowers and fruits during this season (Mantovani and Martins, 1988), which results in the use of rare and unpredictable resources such as insect feces and corpses. Our data support Rockwood's (1975) suggestion that plant phenology may be the most important factor determining seasonal foraging intensity in tropical species of *Atta*.

Cyphomyrmex has long been considered the most primitive attine genus, mainly because it was once believed that *C. rimosus* was the only attine species that did not cultivate fungi (Schultz and Meier, 1995). Although it is currently known that *C. rimosus* and a number of other related species cultivate an easily overlooked yeast phase of the fungus, the notion that *Cyphomyrmex* is primitive has persisted (e.g., Wilson, 1971; Hölldobler and Wilson, 1990). However, the most recent accepted attine phylogeny (Schultz and Meier, 1995) has shown that mycelium cultivation is a plesiomorphic character and that yeast cultivation is derived within the Attini. After Schultz and Meier's work, *Cyphomyrmex* changed from its previous basal position to a more intermediate one. With these shifts in the internal phylogeny of the tribe Attini, some trends accepted by attine experts became less clear, but yet valid, such as the gradual increase in body size and polymorphism of workers, colony size, and complexity of the nest structure, as well as the use of fresh vegetation (see review in Hölldobler and Wilson, 1990). Not only are large mandibles required to cut tough plant parts such as leaves, but the workers have also to be polymorphic because larger individuals are unable to care for the minute fungi within the nest. In fact *Atta* and *Acromyrmex* are the largest, most polymorphic and most advanced attine genera, and use mainly leaves as fungal substrate (Hölldobler and Wilson, 1990 and citations within). Therefore the use of soft plant parts by lower attines reported here may reflect a size constraint of the workers rather than a preference (see also Leal and Oliveira, 1998).

Our ecological data suggest that *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus* and *Myrmicocrypta* are the more primitive genera, whereas *Sericomyrmex* and *Trachymyrmex* would be intermediate ones. Both groups prefer flowers and fruits as fungal substrate, but when these plant parts become rare in the dry season, the first group uses more non-plant items, while the second collects vegetative plant parts. The foraging distances are greater in the intermediate group than in the primitive one, and the *Trachymyrmex* may occasionally climb on trees to cut the flowers. The other lower attine genera not studied here – *Apterostigma* and *Mycetosoritis* – would probably be included in the primitive group, and *Mycetophylax* in the intermediate one (Hölldobler and Wilson, 1990, Mayhé-Nunes, 1995). Finally, a third and more advanced group would be formed by the leaf-cutting ants *Acromyrmex* and *Atta*, together with the parasite *Pseudoatta*. This proposed trend agrees with the attine phylogeny proposed by Schultz and Meier (1995). The foraging activity and load capacity during wet and dry season, colony and worker size, as well as other aspects of the natural history and ecology of attines, are currently under investigation in the cerrado vegetation.

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