

Original Article

External and internal architecture of nests of fungus-growing ants of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex* (Hymenoptera: Formicidae)

Arquitetura externa e interna dos ninhos de formigas cultivadoras de fungo dos gêneros *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta* e *Trachymyrmex* (Hymenoptera: Formicidae)

A. A. Moreira^a , O. C. Bueno^b , R. S. Camargo^c , M. A. Castellani^a , S. A. Leite^a , J. C. Zanuncio^d , J. A. Sabattini^e , R. C. A. L. Paula^a , R. N. S. Lemos^f , B. S. Coelho^a  and N. C. Oliveira^g 

^aUniversidade Estadual do Sudoeste da Bahia – UESB, Departamento de Fitotecnia e Zootecnia, Vitória da Conquista, BA, Brasil

^bUniversidade Estadual Paulista – UNESP, Centro de Estudos de Insetos Sociais, Rio Claro, SP, Brasil

^cUniversidade Estadual Paulista, Departamento de Proteção Vegetal, Botucatu, SP, Brasil

^dUniversidade Federal de Viçosa, Departamento de Entomologia/BIOGRO, Viçosa, MG, Brasil

^eNational University of Entre Rios, National Council for Scientific and Technical Research, School of Agriculture Science, Department of Ecology, Oro Verde, Argentina

^fUniversidade Estadual do Maranhão, São Luís, MA, Brasil

^gUniversidade do Estado de Santa Catarina – UDESC, Centro de Ciências Agroveterinárias – CAV, Departamento de Agronomia, Lages, SC, Brasil

Abstract

Studying the nest structures of fungus-growing ants of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex* is essential to understanding their ecological role. Structural variations affect adaptation of these ants and their impact on agriculture and forest ecosystems. The internal and external structures of 49 fungus-growing ant nests were marked over three months, with four, seven, 31, four, and three nests, respectively, of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex* (Hymenoptera: Formicidae: Attini) were described. The study was conducted in the João Dias da Silveira Campus (Bela Vista) of the São Paulo State University (UNESP) in Rio Claro, São Paulo state, Brazil (22°23'73" S and 47°32'53" W). Forty-nine nests were marked over three months, with four, seven, 31, four, and three nests, respectively, of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex*. Four spherical chambers were observed in *Cyphomyrmex* nests, with height, width, length, and depth, respectively, of 2.8 cm, 2.5 cm, and 2.1 cm, and 15 cm to 30 cm. A single spherical chamber at a depth from 10 to 25 cm was observed in a *Mycetarotes* sp. nest and in each of the 31 nests of *Mycocepurus* sp. and *Myrmicocrypta* sp., with height, width, length, and depth, respectively, of 3.6 cm, 4.5 cm, and 4.1 cm, and 10 to 110 cm; and 5 cm, 5.9 cm, 6.3 cm, and 10 cm to 72 cm. The number of fungus chambers ranged from one to four per *Trachymyrmex* sp. nest, at depths between 15 cm and 205 cm and height, width, and length, respectively, of 3.9 cm, 7.2 cm, and 7.9 cm. Variations in the internal and external structures of Attini ant nests indicate that they should be considered to understand the ecology of these insects

Keywords: ant ecology, forest ecosystems, nest architecture.

Resumo

O estudo das estruturas dos ninhos de formigas cultivadoras de fungo dos gêneros *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta* e *Trachymyrmex* é essencial para compreender seu papel ecológico. As variações estruturais afetam a adaptação dessas formigas e seu impacto na agricultura e nos ecossistemas florestais. As estruturas internas e externas de 49 ninhos de formigas cultivadoras de fungo foram marcadas ao longo de três meses, sendo descritos, respectivamente, quatro, sete, 31, quatro e três ninhos dos gêneros *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta* e *Trachymyrmex* (Hymenoptera: Formicidae: Attini). O estudo foi realizado no Campus João Dias da Silveira (Bela Vista) da Universidade Estadual Paulista (UNESP), em Rio Claro, estado de São Paulo, Brasil (22°23'73" S e 47°32'53" W). Nos ninhos de *Cyphomyrmex*, foram observadas quatro câmaras esféricas, com altura, largura, comprimento e profundidade, respectivamente, de 2,8 cm, 2,5 cm, 2,1 cm e de 15 cm a 30 cm. Em um ninho de *Mycetarotes* sp. e em cada um dos 31 ninhos de *Mycocepurus* sp. e *Myrmicocrypta* sp., foi

*e-mail: camargosauva@gmail.com

Received: February 11, 2025 – Accepted: April 22, 2025



This is an Open Access article distributed under the terms of the Creative Commons Attribution license (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

observada uma única câmara esférica a uma profundidade de 10 a 25 cm, com altura, largura, comprimento e profundidade, respectivamente, de 3,6 cm, 4,5 cm, 4,1 cm e de 10 cm a 110 cm; e 5 cm, 5,9 cm, 6,3 cm e de 10 cm a 72 cm. O número de câmaras de fungo variou de uma a quatro por ninho de *Trachymyrmex* sp., com profundidades entre 15 cm e 205 cm e altura, largura e comprimento, respectivamente, de 3,9 cm, 7,2 cm e 7,9 cm. As variações nas estruturas internas e externas dos ninhos das formigas Attini indicam que essas características devem ser consideradas para compreender a ecologia desses insetos.

Palavras-chave: ecologia de formigas, ecossistemas florestais, arquitetura de ninhos

1. Introduction

Ant nests are primarily located underground, as well as in rotten logs, plant parts, and under leaves (Weber, 1945, 1972; Pereira-da-Silva et al., 1981; Mayhé-Nunes, 1995a). Soil excavated from chambers and channels by ant workers, along with plant debris such as straw, plant leaves, and/or twigs, forms the external appearance of Attini ant nests, with only one entrance hole in species of more primitive genera (Weber, 1945, 1972; Pereira-da-Silva et al., 1981; Mayhé-Nunes, 1995a).

Some species of leaf-cutting ants of the genus *Acromyrmex* and all of the genus *Atta* deposit soil in mounds above the nest underground, facilitating their identification in the field. An external mound of soil was also reported for species of primitive genera such as *Mycetarotes*, *Mycocepurus*, *Sericomyrmex*, and *Trachymyrmex* (Mayhé-Nunes, 1995a; Leal, 1998). Species of these genera supposedly use a wide variety of organic matter as substrate for their fungus gardens, including arthropod feces, wood pellets, insect cadavers, seeds, flower parts, dry leaves, and other plant debris (Mann, 1916; Weber, 1941, 1945, 1947, 1966, 1968, 1969; Hölldobler and Wilson, 1990; Mueller et al., 2005; Santos and Sousa Souto, 2023; Lutinski et al., 2023; Oliveira et al., 2024).

Chambers with fungus culture, workers, brood, and queen; and others with soil or waste (exhausted plant residues, depleted fungus, and ant cadavers), as well as channels or tunnels connecting one chamber to another and to the external area, characterize leaf-cutting ant nests of the genera *Acromyrmex* and *Atta* (Mariconi, 1970).

Waste chambers are found in nests of different leaf-cutting ant species, including *Acromyrmex balzani*, *Acromyrmex fracticornis*, *Acromyrmex landolti*, *Acromyrmex lobicornis*, and *Acromyrmex striatus*, and *Atta colombica*, *Atta laevigata*, *Atta sexdens*, and *Atta texana* (Wheeler, 1907; Gonçalves, 1961; Haines, 1978; Fowler, 1979; Von Ihering, 1984; Waller and Moser, 1990; Fargi-Brener, 2000). Waste inside colonies can increase the proliferation of pathogenic bacteria and fungi attracting other animals, while its deposition outside the colony reduces the energy expenditure of chamber excavation and the humidity for the symbiotic fungus (Haines, 1978). Deposition of waste externally is positively correlated with cleaning behavior and elimination of pathogenic microorganisms (Diehl-Fleig and Araujo, 1996). However, waste deposited externally by ants can attract other organisms (Weber, 1972), such as *Apterostigma* sp., *Cyphomyrmex rimosus*, *Odontomachus bauri*, *Pheidole fallax*, and *Pheidole radoszkowskii*, which collected seeds and fruit pieces in the waste of *Atta cephalotes* (Roberts and Heithaus, 1986).

The structure of *Atta* nests is the greatest complexity among the Attini, with more than 7,000 chambers and depths of up to 8 meters for *Atta laevigata* (Moreira et al., 2004a), with

internal variations in the shape and location of waste and fungus chambers relative to the external area. This shape of *A. sexdens* nests is semi-ellipsoidal with arm-like extensions in the waste chambers, both under the mound of loose soil (Pretto, 1996), while those of *A. laevigata* and *A. bisphaerica* are spherical (Moreira et al., 2004a, b). Variations in the structure and external shape of nests are used to identify species and subspecies of *Acromyrmex*, although similar nests are reported for different species of this genus (Gonçalves, 1967; Pacheco and Berti-Filho, 1987).

The structural complexity of nests of primitive Attini, such as those of *Cyphomyrmex*, *Mycetarotes*, and *Mycetophylax*, with few and superficial chambers not exceeding 20 cm deep, differs from those of *Atta* and *Acromyrmex* (Mayhé-Nunes, 1995a). Chambers of *Mycetosoritis* and *Mycocepurus* are found at 30 to 120 cm deep, and those of *Trachymyrmex* spp. and *Trachymyrmex fuscus* at 2.7 to 59 cm and 111 to 208 cm deep, respectively, generally with three chambers and a single entrance (Araújo and Della Lucia, 1997). The objective of this study was to describe the external and internal architecture of ants of fungus-growing ant of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex* (Hymenoptera: Formicidae) in Brazil.

2. Material and Methods

2.1. Study genera and location

The internal and external structures of ant nests of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex*, all fungus-growing Attini, were studied in the João Dias da Silveira Campus (Bela Vista) of the São Paulo State University (UNESP) in Rio Claro, São Paulo state, Brazil (22°23'73" S and 47°32'53" W).

2.2. Nest mapping

Attini workers were followed to the entrance holes of their nests, which were marked with stakes bearing an identification number. Some workers from each nest were collected after offering oats to them while they returned to their respective nests. Forty-nine nests were marked over three months, with four, seven, 31, four, and three nests, respectively, of the genera *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, and *Trachymyrmex* in Rio Claro, São Paulo state, Brazil.

2.3. Identification

Ant workers collected were placed in jars with 80% alcohol, taken to the laboratory, and identified at the genus level using keys (Weber, 1972; Bolton, 1995; Mayhé-Nunes,

1995a). Specimens of these workers were sent to Dra. Ana Eugênia de Carvalho C. Farinha of the Biological Institute of São Paulo, Brazil for identification at species level and deposited in the Adolpho Hempel Entomological Collection of that institution.

2.4. External architecture of the nests

The external area of the nests was calculated by measuring the loose soil mound, using the greatest length and width. The distance between the soil mounds and the nest entrance was not recorded, as only observations were made. The external area of some nests was measured, and their entrance holes photographed.

2.5. Internal architecture of the nests

Trenches with a width of 0.70 m and with variable depth depending on the genus of Attini were manually excavated to describe the internal structure of their nests. Soil layers were removed after opening the trench towards the nest, and the excavation deepened as necessary. The channels were marked with the application of talcum powder using a manual formicide applicator, facilitating the location of the chambers of each nest.

The number, width, height, length, and depth of the chambers of each leaf-cutting ant nest were measured. The material in the chambers, including fungus and larvae, pupae and workers of the ants collected and transferred to artificial nests in the laboratory.

3. Results

3.1. External structure of the nests

The apparent area of loose soil in one of the four nests of *Cyphomyrmex* sp. was 49 cm² with a height of 5 cm and an its external structure with small soil granules forming a low mound with an orifice at the top.

Small soil granules forming a small mound with an orifice at the top characterized the external structure of *Mycetarotes* (Figure 1A).

Entrance orifices surrounded by soil granules or dry leaves and small mounds of loose soil were observed in the nests of *Mycocepurus* sp. (Figure 1B).

An entrance orifice surrounded by soil granules was observed in a *Myrmicocrypta* sp. nest.

The apparent area of loose soil of *Trachymyrmex* sp. nests ranged from 300 to 374 cm², and the diameter of

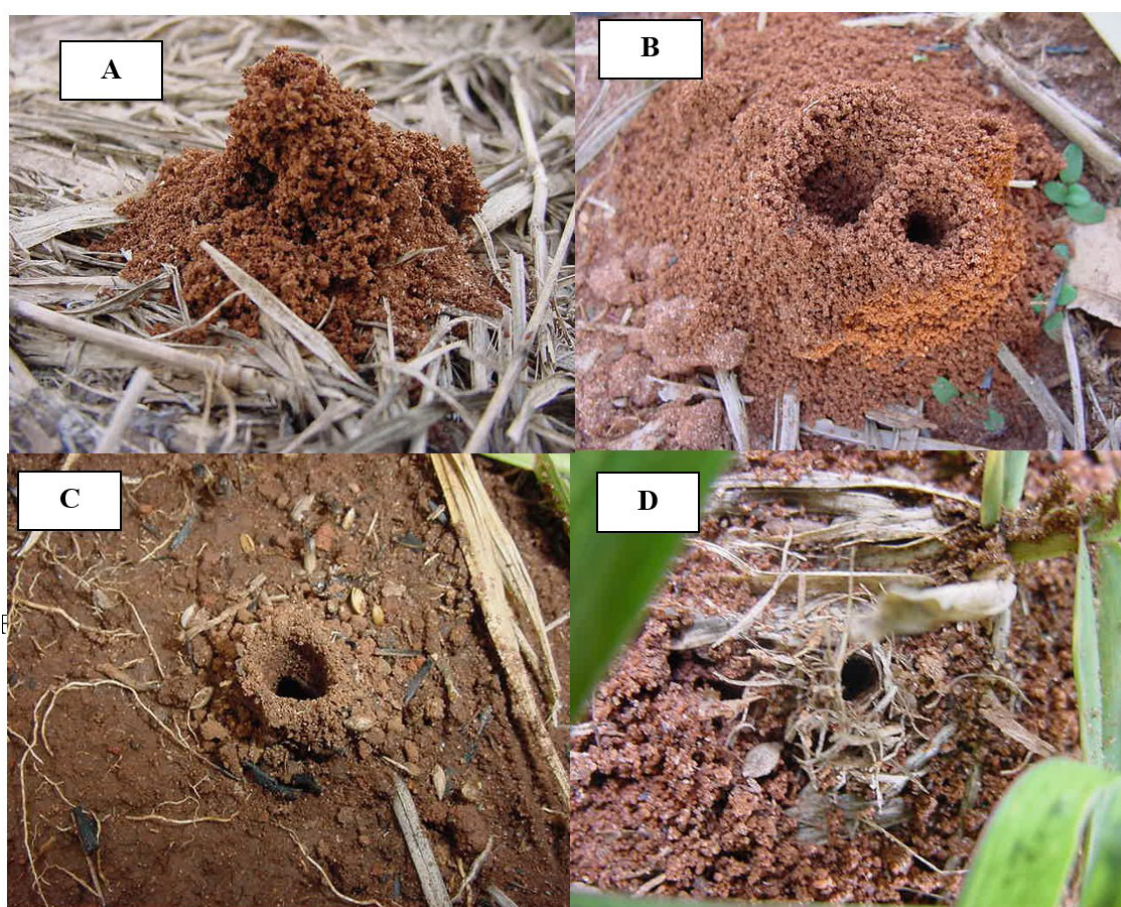


Figure 1. External aspects of ant nests of the genera *Mycetarotes* (A), *Mycocepurus* (B), and *Trachymyrmex* (C and D) (Hymenoptera: Formicidae).

their entrance orifices from 2.5 to 4 cm. One to three entrance orifices, surrounded by soil granules or dry leaves (Figure 1C and D), and small mounds of loose soil were observed on e nests of a species of this genus.

3.2. Internal structure of the nests

The chambers of the four *Cyphomyrmex* sp. nests (Table 1) were spherical, with a height, width, length, and depth of 2.8 cm, 2.5 cm, 2.1 cm, and 15 to 30 cm, respectively

(Table 1). Part of the fungus garden was suspended from roots with the other part at the base of the chamber.

A single spherical chamber, between 10 cm and 25 cm deep, with a height, width, and length of 3.6 cm, 4.5 cm, and 4.1 cm, respectively, and channels with a diameter of 0.5 cm, was observed in the nests of *Mycetarotes* sp. (Table 2 and Figure 2A).

A single fungus chamber per nest (n= 31), spherical in shape, with a height, width, length, and depth of 3.6 cm, 4.5 cm, 4.1 cm, and 10 to 110 cm, respectively, and channels

Table 1. Number of chambers (N), chamber (C), and height (H), width (W), length (L), and depth (D), in centimeters, of the nest chambers of the ant species of the genera *Cyphomyrmex* sp., *Myrmicocrypta* sp., and *Trachymyrmex* sp. in the Rio Claro region, São Paulo state, Brazil.

Genus Nests	N	C	Chamber			D
			H	W	L	
CY121			3.0	4.0	2.0	15.0
<i>Cyphomyrmex</i> sp. CY122			3.5	3.0	3.0	30.0
CY123			1.0	1.0	1.0	30.0
CY124			3.5	2.0	2.5	20.0
Mean			2.8	2.5	2.1	23.8
Median			3.3	2.5	2.3	25.0
Maximum			3.5	4.0	3.0	30.0
Minimum			1.0	1.0	1.0	15.0
MR105			6.0	7.5	8.0	35.0
<i>Myrmicocrypta</i> sp. MR106			6.5	6.0	7.0	30.0
MR107			0.5	1.0	1.0	10.0
MR108			7.0	9.0	9.0	72.0
Mean			5.0	5.9	6.3	36.8
Median			6.3	6.8	7.5	32.5
Maximum			7.0	9.0	9.0	72.0
Minimum			0.5	1.0	1.0	10.0
TR 118	4.0	1.0	2.0	3.5	2.5	20
<i>Trachymyrmex</i> sp.		2.0	5.0	9.0	8.0	30
		3.0	5.5	12	16	160
		4.0	6.5	16	18.5	205
TR 119	2.0	1.0	2.5	2.5	3.0	15
		2.0	2.0	4.0	3.5	43
TR 120	1.0	1.0	3.5	3.5	4.0	30
Mean	1.0	2.0	3.9	7.2	7.9	71.9
Median	0.0	2.0	3.5	4.0	4.0	30
Maximum	4.0	4.0	6.5	16	18.5	205
Minimum	0.0	1.0	2.0	2.5	2.5	15

Table 2. Height (H), width (W), length (L), and depth (D.), in centimeters, of the nest chambers of ants of the genera *Mycocepurus* sp. and *Mycetarotes* sp. in the Rio Claro region, São Paulo state, Brazil.

Nests	<i>Mycocepurus</i> sp.				Nests	<i>Mycetarotes</i> sp.			
	H	W	L	D		H	W	L	D
MP119	2.0	2.0	1.5	14	MT113	5	4	3	10
MP120	3.5	3.0	3.0	17	MT114	5	4	3	12
MP121	1.5	2.0	1.5	25	MT115	2	3	3	12
MP122	2.5	3.5	3.0	20	MT116	2	2.5	2.5	16
MP123	3.5	3.0	3.0	14	MT117	1.5	1.5	0.5	25
MP124	2.5	4.0	4.0	20	MT118	4	4.5	5	20
MP125	4.5	6.0	5.5	25	MT119	4	4	4	17
MP126	2.0	2.5	2.0	20					
MP127	3.0	5.0	3.5	28					
MP128	6.0	5.0	5.5	10					
MP129	4.5	4.0	4.5	19					
MP130	5.0	6.5	6.5	20					
MP131	3.5	2.0	3.5	15					
MP132	2.0	2.5	2.0	20					
MP133	2.0	2.5	2.0	34					
MP134	7.5	10.0	8.0	85					
MP135	2.0	2.0	2.0	40					
MP136	2.0	4.0	2.0	42					
MP137	7.0	9.0	9.0	87					
MP138	6.0	8.0	8.0	110					
MP139	2.0.0	3.5	2.5	15					
MP140	3.5	5.0	5.0	60					
MP141	4.0	5.0	4.0	85					
MP142	4.5	6.0	5.0	95					
MP143	4.0	5.0	4.5	80					
MP144	3.5	6.5	6.0	10					
MP145	3.5	6.0	5.0	20					
MP146	3.0	5.0	5.0	28					
MP147	2.0	2.5	1.5	20					
MP148	4.5	6.0	7.0	26					
MP149	5.0	4.0	3.0	15					
Mean	3.6	4.5	4.1	36.1	Mean	3.4	3.4	3.0	16.0
Median	3.5	4.0	4.0	20.0	Median	4.0	4.0	3.0	16.0
Maximum	7.5	10.0	9.0	110.0	Maximum	5.0	4.5	5.0	25.0
Minimum	1.5	2.0	1.5	10.0	Minimum	1.5	1.5	0.5	10.0

with a diameter of 0.5 cm, were observed in the nests of *Mycocepurus* sp. (Table 2 and Figure 2B).

A single spherical chamber with a height, width, length, and depth of 5 cm, 5.9 cm, 6.3 cm, and 10 to 72 cm, respectively, was observed per nest of *Myrmicocrypta* sp. (Table 1).

Four fungus chambers with an ellipsoidal shape, flat base, and a height, width, length, and depth of 3.9 cm, 7.2 cm, 7.9 cm, and 15 to 205 cm, respectively, with the fungus garden at the base or suspended from the top, were observed in each of the three *Trachymyrmex* sp. nests (Table 1) (Figure 2C, D).

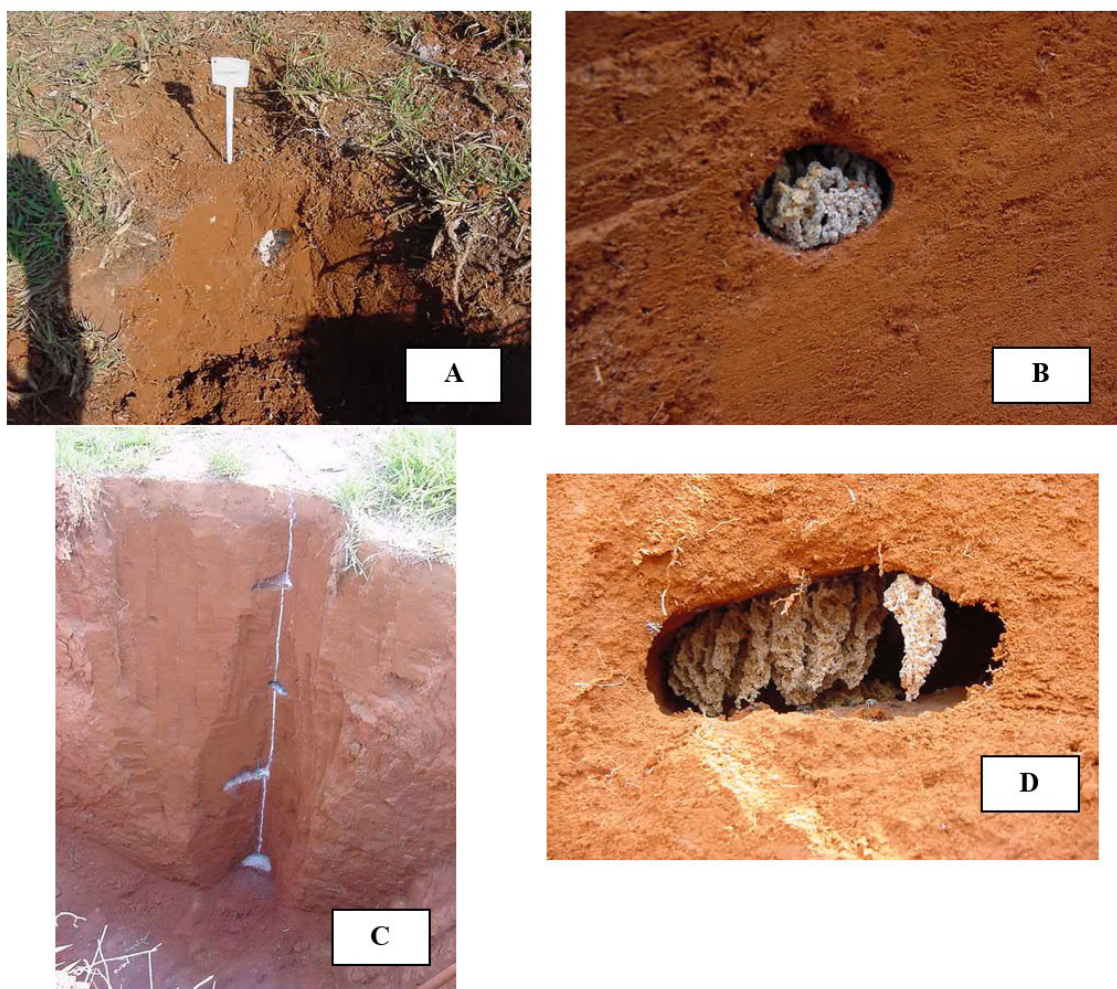


Figure 2. Internal structure of ant nests of the genera *Mycetarotes* (A), *Mycocepurus* (B), and *Trachymyrmex* (C), and the fungus chamber of *Trachymyrmex* (D).

4. Discussion

4.1. External structure of the nests

Soil removed by the workers during the excavation of the chambers and channels in the ground or straw or twigs, along with one small entrance and exit form the external structure of the ant nests were similar to that reported for *Acromyrmex* spp. (Weber, 1972).

The area of loose soil of one of the four nests of *Cyphomyrmex* sp., with 49 cm² and a height of 5 cm, and an external structure with small soil granules forming a small mound and an orifice at the top, is considered simple (Leal et al., 2011; Ramos-Lacau et al., 2012) compared to those of the genera *Acromyrmex* and *Atta* (Wirth et al., 2003; Silva Junior et al., 2010). However, similar structures have been reported, such as a single circular entrance holes without a well-formed mound of loose soil, for *Cyphomyrmex lectus* and *Cyphomyrmex morschi* (Klingenberg et al., 2007) and for species of other Attini ant genera including *Mycocepurus*

Forel, *Mycetarotes* Emery, *Sericomyrmex* Mayr, and *Trachymyrmex* Forel (Mayhé-Nunes 1995a; Leal et al., 2011). However, this differs from that reported for *Cyphomyrmex transversus* and *Cyphomyrmex cornutus*, with distinct nesting habits (Adams and Longino, 2007; Ramos-Lacau et al., 2012). Additionally, large masses of aggregated soil suspended in lower arboreal parts formed nests of *Cyphomyrmex cornutus* on the Atlantic slopes of Costa Rica (Adams and Longino, 2007). The genus *Cyphomyrmex* includes species, such as *Cyphomyrmex longiscapus*, considered ideal models for studies of behavior, cultivation specificity, ecology, mating frequency, etc. (Schultz et al., 2002).

Small soil granules forming a low mound with a hole at the top are the external structure of *Mycetarotes* sp. nests. This is similar to that reported for nests of this ant, with a single shallow chamber, in secondary forest with clay soil in a trail used by humans (Mayhé-Nunes and Lanziotti, 2004). Entrance orifices surrounded by soil granules or dry leaves, and small mounds of loose soil

in *Mycocepurus* sp. nests are similar to those observed for *M. smithii* with a single hole. However, the high density and proximity of nest holes can lead to the mistaken conclusion of multiple ones per nest of this ant (Fernández-Marín et al., 2005), confirming reports of intraspecific variation in nest architecture as scarce and with conflicting data that may be correct (Kempf, 1963). A single entrance hole was also reported in nests of *M. smithii* and *Mycocepurus tardus* in Costa Rica and Trinidad and for *M. goeldii* in Brazil and Guyana (Fernández-Marín et al., 2005).

An entrance hole surrounded by soil granules, observed in a *Myrmicocrypta* sp. nest, agrees to that of *Myrmicocrypta camargoii* (Sosa-Calvo and Schultz, 2010), with an entrance hole surrounded by soil granules and a single shallow spherical chamber below the soil surface.

The area of loose soil visible in *Trachymyrmex* sp. nests, from 300 cm² to 374, with entrance holes between 2.5 and 4 cm in diameter, is similar to that for *T. urichi* (Weber, 1945) and *T. fuscus*, with a single entrance hole shaped like a semi-hardened mud straw (Araujo et al., 2002). *Trachymyrmex* spp. nests are, generally, reported with seven chambers and one or more entrance holes surrounded by soil, reflecting the size of the nests (Weber, 1956, 1966, 1969, 1972). The three-dimensional structure of *T. septentrionalis* nests, described with one to five vertically connected oval chambers a few centimeters below the soil surface (Tschinkel, 2003), agrees with that of *T. fuscus*, a species synonymous to *T. urichi*, with some vertically connected oval chambers a few centimeters below the soil surface (Araujo et al., 2002). Additionally, aspects of nesting are mentioned and used in taxonomic reviews and other general nesting studies (Fernández-Marín et al., 2004; Mayhé-Nunes and Brandão, 2004).

4.2. Internal structure of the nests

A spherical chamber with a height, width, length, and depth of 2.8 cm, 2.5 cm, 2.1 cm, and 15 to 30 cm, respectively, and the fungus garden partially suspended from roots and the remainder at the base in four nests of *Cyphomyrmex* sp., is similar to the structurally simple nests described for *C. transversus*, with a single chamber (Ramos-Lacau et al., 2012). However, variations in this parameter were reported for ants of this genus such as *C. longiscapus* as one of the most unusual among fungus-growing ants, featuring a large entrance hole opening and clay walls often surrounding the nest cavity in a swallow-like style, predominantly in vertical banks along permanent streams (Mueller and Wcislo, 1998).

A single spherical chamber per nest of *Mycetarotes* sp., at a depth of 10 cm to 25 cm, with a height, width, and length of 3.6 cm, 4.5 cm, and 4.1 cm, respectively, differs in diameter but agrees with that of *M. parallelus*, with a single spherical chamber (Luederwaldt, 1918) with a width, height, and depth of 4 to 7 cm, 3 to 4 cm, and 10 cm, respectively, in Viçosa, Minas Gerais state, Brazil (Mayhé-Nunes, 1995b). The reduced diameter of *Mycocepurus* sp. channels is similar to reports for *M. smithii* with a slight downward inclining directly to the chamber and connecting the external and internal areas of the nest of this latter ant, with the fungus garden at the bottom of

the chamber or hanging from grass roots (Luederwaldt, 1918; Mayhé-Nunes, 1995a).

A single spherical fungal chamber in each of the 31 nests of *Mycocepurus* sp., with a height, width, length, and depth of 3.6 cm, 4.5 cm, 4.1 cm, and 10 to 110 cm, respectively, and channels with a diameter of 0.5 cm, confirms variations in these parameters among species of primitive Attini genera. This contrasts with the more complex nests of *Atta*, with greater number of chambers at different depths and up to 7 million workers per nest (Moreira and Forti, 1999; Moreira et al., 2004a).

The number of chambers in *Mycocepurus* sp. nests differs from that reported for *M. goeldii*, up to four chambers at the depths of 60 cm (Leal, 1998) to 120 cm (Luederwaldt, 1918, 1926). However, the width and height of the chambers of species in this genus were similar to the 10 cm and 20 cm, respectively, reported for both *M. goeldii* and *M. tardus* (Luederwaldt, 1918, 1926; Weber, 1972). The fungus garden of *Mycocepurus* sp., hanging from the top, on roots, or at the base of the chamber, is similar to that of *M. goeldii* in Brazil (Luederwaldt, 1918, 1926; Weber, 1972; Mayhé-Nunes, 1995a; Leal 1998).

Spherical chambers in *Myrmicocrypta* sp. nests (5 cm high, 5.9 cm wide, and 6.3 cm long) are similar to that of species of this genus in other locations, with chamber width, height, and depth of 6.5 cm, 5.3 cm, and 5.2 to 11 cm, respectively (Weber, 1937, 1941, 1945, 1968). However, up to two chambers at depths of 25 cm to 62 cm and a maximum volume of 358.2 cm³ of loose soil have been reported for nests of ants of the *Myrmicocrypta* genus in the Brazilian Cerrado (Leal, 1998).

The number of chambers in *Trachymyrmex* sp. nests, one to four, with height, width, length, and depth of 15 cm, 7.2 cm, 7.9 cm, and 15 cm to 205 cm, respectively, are similar to the four chambers at a maximum depth of 118 cm for species of this genus in the Cerrado biome (Leal, 1998). However, a total of six chambers, between 2.5 cm and 59 cm deep, connected to each other by small-diameter circular channels, usually not exceeding 1 cm in *T. fuscus* nests and often perpendicular to the soil surface, have been observed (Mayhé-Nunes, 1995a). One to five oval chambers a few centimeters deep and connected vertically to the soil surface characterize the internal structure of *T. septentrionalis* nests. Four to five chambers were reported for each of the four nests of *T. holmgreni* excavated in the Restinga (Albuquerque et al., 2018).

5. Conclusion

Variations in the external and internal structures of ant nests within the tribe Attini confirm the behavioral and adaptive diversity of these social insects.

A single chamber per *Cyphomyrmex* nest, superficially under the soil or beneath stones and roots, and *Trachymyrmex* nests, with characteristics of primitive and more derived species such as *Acromyrmex* and *Atta*, suggest that the second genus is an intermediate stage in the evolution of nest structure within the Attini tribe. This is significant to understanding nesting strategies of fungus-growing ants.

The ecology and excavation behavior of Attini ants highlight the importance of understanding the external and internal structures of their nests to comprehend their social and ecological interactions in natural and modified habitats.

References

- ADAMS, R.M. and LONGINO, J.T., 2007. Nesting biology of the arboreal fungus-growing ant *Cyphomyrmex cornutus* and behavioral interactions with the social-parasitic ant *Megalomyrmex mondabora*. *Insectes Sociaux*, vol. 54, no. 2, pp. 136-143. <http://doi.org/10.1007/s00040-007-0922-0>.
- ALBUQUERQUE, E.Z., DIEHL-FLEIG, E., DIEHL, E. and MAYHÉ-NUNES, A.J., 2018. Sex investment ratios and natural history observations in a population of *Trachymyrmex holmgreni* (Formicidae) in southern Brazil. *Insectes Sociaux*, vol. 65, no. 2, pp. 297-303. <http://doi.org/10.1007/s00040-018-0614-y>.
- ARAUJO, M.S. and DELLA LUCIA, T.M.C., 1997. Caracterização de ninhos de *Acromyrmex laticeps nigrosetosus* Forel, em povoados de eucalipto em Paraopeba, MG. *Anais da Sociedade Entomológica do Brasil*, vol. 26, no. 1, pp. 205-207. <http://doi.org/10.1590/S0301-80591997000100029>.
- ARAUJO, M.S., DELLA LUCIA, T. and MAYHÉ-NUNES, A.J., 2002. Caracterização de ninhos e atividade forrageadora de *Trachymyrmex fuscus* Emery (Hymenoptera, Formicidae) em plantio de eucalipto. *Revista Brasileira de Zoologia*, vol. 19, no. 2, pp. 419-427. <http://doi.org/10.1590/S0101-81752002000200008>.
- BOLTON, B., 1995. *A new general catalogue for the ants of the world*. Cambridge, MA: Harvard University Press.
- DIEHL-FLEIG, E. and ARAÚJO, A.M., 1996. Haplometrosi and pleometrosis in ant *Acromyrmex striatus* (Hymenoptera: formicidae). *Insectes Sociaux*, vol. 43, no. 1, pp. 47-51. <http://doi.org/10.1007/BF01253955>.
- FARGI-BRENER, A.G., 2000. Leaf-cutting ant nests in temperate environments: mounds, mound damage and nest mortality rate in *Acromyrmex lobicornis*. *Studies on Neotropical Fauna and Environment*, vol. 35, no. 2, pp. 131-138. [http://doi.org/10.1076/0165-0521\(200008\)35:2;1-9;FT131](http://doi.org/10.1076/0165-0521(200008)35:2;1-9;FT131).
- FERNÁNDEZ-MARÍN, H., ZIMMERMAN, J.K. and WCISLO, W.T., 2004. Ecological traits and evolutionary sequence of nest establishment in fungus-growing ants (Hymenoptera, Formicidae, Attini). *Biological Journal of the Linnean Society. Linnean Society of London*, vol. 81, no. 1, pp. 39-48. <http://doi.org/10.1111/j.1095-8312.2004.00268.x>.
- FERNÁNDEZ-MARÍN, H., ZIMMERMAN, J.K., WCISLO, W.T. and REHNER, S.A., 2005. Colony foundation, nest architecture and demography of a basal fungus-growing ant, *Mycocepurus smithii* (Hymenoptera, Formicidae). *Journal of Natural History*, vol. 39, no. 20, pp. 1735-1743. <http://doi.org/10.1080/00222930400027462>.
- FOWLER, H.G., 1979. Environmental correlates of the foraging of *Acromyrmex crassispinus*. *Ciencia e Cultura*, vol. 31, pp. 879-882.
- GONÇALVES, C.R., 1961. O gênero *Acromyrmex* no Brasil (Hymenoptera: formicidae). *Studia Entomologica*, vol. 4, pp. 113-180.
- GONÇALVES, C.R., 1967. As formigas cortadeiras. *Revista Brasileira de Biologia*, vol. 3, pp. 5-11.
- HAINES, B.L., 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica*, vol. 10, no. 4, pp. 270-277. <http://doi.org/10.2307/2387679>.
- HOLLOBLER, B. and WILSON, E.O., 1990. *The ants*. Cambridge, MA: Belknap Press. <http://doi.org/10.1007/978-3-662-10306-7>.
- KEMPE, W.W., 1963. A review of the ant genus *Mycocepurus* Forel, 1983 (Hymenoptera: formicidae). *Studia Entomologica*, vol. 6, pp. 417-432.
- KLINGENBERG, C., BRANDÃO, C.R.F. and ENGELS, W., 2007. Primitive nest architecture and small monogynous colonies in basal Attini inhabiting sandy beaches of southern Brazil. *Studies on Neotropical Fauna and Environment*, vol. 42, no. 2, pp. 121-126. <http://doi.org/10.1080/01650520601065509>.
- LEAL, I.R. 1998. *Ecologia e história natural de formigas Attini em vegetação de cerrado*. Campinas: Instituto de Biologia, Universidade Estadual de Campinas, 142 p. Tese (Doutorado em Ciências Biológicas, Área de Concentração: Ecologia).
- LEAL, I.R., SILVA, P.S.D. and OLIVEIRA, P.S., 2011. Natural history and ecological correlates of fungus-growing ants (Formicidae: Attini) in the Neotropical cerrado savanna. *Annals of the Entomological Society of America*, vol. 104, no. 5, pp. 901-908. <http://doi.org/10.1603/AN11067>.
- LUEDERWALDT, H., 1918. Notas myrmecológicas. *Revista do Museu Paulista*, vol. 10, pp. 29-64.
- LUEDERWALDT, H., 1926. Observações biológicas sobre formigas brasileiras, especialmente do Estado de São Paulo. *Revista do Museu Paulista*, vol. 14, pp. 185-304.
- LUTINSKI, J.A., DORNELES, F.E., GUARDA, C., LUTINSKI, C.J., BUSATO, M.A., GIOVENARDI, R. and GARCIA, F.R.M., 2023. Ant diversity (Hymenoptera: Formicidae) in Turvo State Park, municipality of Derrubadas, state of Rio Grande do Sul, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 83, pp. e239642. <http://doi.org/10.1590/1519-6984.239642>. PMID:34133487.
- MANN, W.M., 1916. The ants of Brazil. *Bulletin of the Museum of Comparative Zoology at Harvard College*, vol. 60, pp. 399-490.
- MARICONI, F.A.M., 1970. *As Saúvas*. São Paulo: Agronômica Ceres. 167 p.
- MAYHÉ-NUNES, A.J. 1995a. *Filogenia de los Attini (Hym., Formicidae): un aporte al conocimiento de las hormigas fungívoras*. Sartenejas: Universidad Simón Bolívar, 274 p. Tesis (Doctor em Ciencias Biológicas).
- MAYHÉ-NUNES, A.J., 1995b. Sinopse do gênero *Mycetarotes* (Hym., Formicidae), com a descrição de duas espécies novas. *Boletim de Entomología Venezolana*, vol. 10, pp. 197-205.
- MAYHÉ-NUNES, A.J. and BRANDÃO, C.R.F., 2004. Revisionary notes on the fungus-growing ant genus *Mycetarotes* Emery (Hymenoptera, Formicidae). *Revista Brasileira de Entomologia*, vol. 50, no. 4, pp. 463-472. <http://doi.org/10.1590/S0085-56262006000400005>.
- MAYHÉ-NUNES, A.J. and LANZIOTTI, A., 2004. Description of the female and male of *Mycetarotes carinatus* (Hymenoptera: formicidae). *Revista de Biología Tropical*, vol. 52, no. 1, pp. 109-114. <http://doi.org/10.15517/rbt.v52i1.14758>. PMID:17357406.
- MOREIRA, A.A. and FORTI, L.C., 1999. Comparação entre o volume externo e interno de ninhos de *Atta laevigata* (Hymenoptera: formicidae). *Revista Árvore*, vol. 23, pp. 355-358.
- MOREIRA, A.A., FORTI, L.C., ANDRADE, A.P.P., BOARETTO, M.A.C. and LOPES, J.F.S., 2004a. Nest Architecture of *Atta laevigata* (F. Smith, 1858) (Hymenoptera: formicidae). *Studies on Neotropical Fauna and Environment*, vol. 39, no. 2, pp. 109-116. <http://doi.org/10.1080/01650520412331333756>.
- MOREIRA, A.A., FORTI, L.C., BOARETTO, M.A.C., ANDRADE, A.P.P., LOPES, J.F.S. and RAMOS, V.M., 2004b. External e internal structure of *Atta bisphaerica* Forel (Hymenoptera: formicidae). *Journal of Applied Entomology*, vol. 128, no. 3, pp. 204-211. <http://doi.org/10.1111/j.1439-0418.2004.00839.x>.
- MUELLER, U.G. and WCISLO, W.T., 1998. Nesting biology of the fungus-growing ant *Cyphomyrmex longiscapus* Weber (Attini,

- Formicidae). *Insectes Sociaux*, vol. 45, no. 2, pp. 181-189. <http://doi.org/10.1007/s000400050078>.
- MUELLER, U.G., GERARDO, N.M., SCHULTZ, T.R., AANEN, D.K. and SIX, D., 2005. The evolution of agriculture in insects. *Annual Review of Ecology, Evolution, and Systematics*, vol. 36, no. 1, pp. 563-595. <http://doi.org/10.1146/annurev.ecolsys.36.102003.152626>.
- OLIVEIRA, F.M.M., DEMOLIN-LEITE, G.L., VELOSO, R.V.S., GUANABENS, R.E.M., SILVA, Y.O.R. and AMARAL, F.L., 2024. Distribution pattern of arthropods and their ecological interactions on the leaf surfaces of *Terminalia argentea* saplings. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 84, pp. e281588. <http://doi.org/10.1590/1519-6984.281588>. PMID:38896730.
- PACHECO, P. and BERTI-FILHO, E., 1987. Formigas quenquêns. In: P. PACHECO and E. BERTI-FILHO, eds. *Formigas cortadeiras e o seu controle*. Piracicaba: ESALQ, pp. 3-17.
- PEREIRA-DA-SILVA, V., FORTI, L.C. and CARDOSO, L.G., 1981. Dinâmica populacional e caracterização dos ninhos de *Acromyrmex coronatus* (Fabricius, 1804) (Hymenoptera: formicidae). *Revista Brasileira de Entomologia*, vol. 25, pp. 87-93.
- PRETTO, D.R., 1996. *Arquitetura dos túneis de forrageamento e do ninho de Atta sexdens rubropilosa* Forel, 1908 (Hymenoptera - Formicidae), dispersão de substrato e dinâmica do inseticida na colônia. Botucatu: Faculdade de Ciências Agronômicas, Universidade Estadual Paulista, 110 p. Dissertação (Mestrado em Proteção de Plantas).
- RAMOS-LACAU, L.S., SILVA, P.S.D., LACAU, S., DELABIE, J.H. and BUENO, O.C., 2012. Nesting architecture and population structure of the fungus-growing ant *Cyphomyrmex transversus* (Formicidae: Myrmicinae: Attini) in the Brazilian coastal zone of Ilhéus, Bahia. *Annales de la Société Entomologique de France*, vol. 48, no. 3-4, pp. 439-445. <http://doi.org/10.1080/00379271.2012.10697789>.
- ROBERTS, J.T. and HEITHAUS, E.R., 1986. Ants rearrange the vertebrate-generated seed shadow of a Neotropical fig tree. *Ecology*, vol. 67, no. 4, pp. 1046-1051. <http://doi.org/10.2307/1939827>.
- SANTOS, R.S. and SOUSA-SOUTO, L., 2023. Nest refuse of *Acromyrmex balzani* (Hymenoptera: Formicidae) increases the plant vigor in *Turnera subulata* (Turneraceae). *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 83, pp. e244732. <http://doi.org/10.1590/1519-6984.244732>. PMID:34161460.
- SCHULTZ, T.R., SOLOMON, S.A., MUELLER, U.G., VILLESSEN, P., BOOMSMA, J.J., ADAMS, R.M. and NORDEN, B., 2002. Cryptic speciation in the fungus-growing ants *Cyphomyrmex longiscapus* Weber and *Cyphomyrmex muelleri* Schultz and Solomon, new species (Formicidae, Attini). *Insectes Sociaux*, vol. 49, no. 4, pp. 331-343. <http://doi.org/10.1007/PL00012657>.
- SILVA JUNIOR, M.R., CASTELLANI, M.A., MOREIRA, A.A., D'ESQUIVEL, M., SOSA-CALVO, J. and SCHULTZ, T.R., 2010. Three remarkable new fungus-growing ant species of the genus *Myrmicocrypta* (Hymenoptera: Formicidae), with a reassessment of the characters that define the genus and its position within the Attini. *Annals of the Entomological Society of America*, vol. 103, no. 2, pp. 181-195. <http://doi.org/10.1603/AN09108>.
- TSCHINKEL, W.R., 2003. Subterranean ant nests: trace fossils past and future? *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 192, no. 1-4, pp. 321-333. [http://doi.org/10.1016/S0031-0182\(02\)00690-9](http://doi.org/10.1016/S0031-0182(02)00690-9).
- VON IHERING, H., 1984. Die Ameisen von Rio Grande do Sul. *Berliner Entomologische Zeitschrift*, vol. 39, pp. 321-446.
- WALLER, D.A. and MOSER, J.C., 1990. Invertebrate enemies and nest associates of the leaf-cutting ant *Atta texana* (Buckley) (Formicidae, Attini). In: R.K. VANDER MEER, K. JAFFÉ and A. CEDEÑO, eds. *Applied Myrmecology – a world perspective*. Boulder: Westview Press, pp. 255-273.
- WEBER, N.A. 1969. A comparative study of the nests, gardens and fungi of the fungus-growing ants, Attini. In: E. ERNST, and E. AL, eds. VI Congress. Bern: Organizing Committee of the VI Congress IUSSI, pp. 299-307.
- WEBER, N.A., 1937 [viewed 11 February 2025]. The biology of the fungus-growing ants, Part II: Nesting habits of the Bachaco (*Atta cephalotes*). *Tropical Agriculturist* [online], vol. 14, pp. 8. Available from <https://journals.sta.uwi.edu/ojs/index.php/ta/article/view/5696>
- WEBER, N.A., 1941. The biology of the fungus-growing ants, Part VII: The Barro Colorado Island, Canal Zone, species. *Revista de Etologia*, vol. 12, pp. 93-130.
- WEBER, N.A., 1945. The biology of the fungus-growing ants. Part 8. The Trinidad, B.W.I. Species. *Revista de Etologia*, vol. 16, pp. 1-88.
- WEBER, N.A., 1947. Lower Orinoco River fungus-growing ants (Hymenoptera: Formicidae, Attini). *Boletín de Entomología Venezolana*, vol. 6, pp. 143-161.
- WEBER, N.A., 1956. Fungus-growing ants and their fungi: *trachymyrmex septentrionalis*. *Ecology*, vol. 37, no. 1, pp. 150-161. <http://doi.org/10.2307/1929678>.
- WEBER, N.A., 1966. Fungus-growing ants. *Science*, vol. 153, no. 3736, pp. 587-604. <http://doi.org/10.1126/science.153.3736.587>. PMID:17757227.
- WEBER, N.A., 1968. Tobago Island fungus-growing ants (Hymenoptera: formicidae). *Entomological News*, vol. 74, pp. 141-145.
- WEBER, N.A., 1972. *Gardening ants, the attines*. Philadelphia: American Philosophical Society, 146 p.
- WHEELER, W.M., 1907. The fungus-growing ants of North America. *Bulletin of the American Museum of Natural History*, vol. 23, pp. 669-807.
- WIRTH, R., BEYSCHLAG, W., RYEL, R., HERZ, H. and HÖLLDOBLER, B., 2003. Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama. In: J.G. CANADELL, G. HELDMAIER, R.B. JACKSON, D.F. LEVIA, E.-D. SCHULZE, U. SOMMER and D.A. WARDLE, eds. *Ecological studies: analysis and synthesis*. Berlin: Springer. <http://doi.org/10.1007/978-3-662-05259-4>.