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The nest architecture of the ant, *Pheidole oxyops* Forel, 1908 (Hymenoptera: Formicidae)

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Abstract *Pheidole oxyops* builds subterranean nests, with an external architecture that is distinctive and easily recognizable by its wide and specific entrance hole, measuring up to 12.2 cm in diameter, denoting a pitfall-trap. In order to study the nests' internal architecture, seven nests were excavated; four were identified with neutral talc, while the others were cast in cement and then excavated. Measurements were made in order to gain a better understanding of their structures, and a photographic documentation was obtained as well. The excavations revealed that the nests are perpendicular relative to the ground, beginning with a cylindrical channel with a mean length of 13.5 cm, containing irregular formations, and whose diameter becomes progressively narrower until the first chamber is formed. As the channel continues, dish-like chambers appear, interconnected by channels that become progressively narrower and longer, while the chambers are arranged at greater distances from each other as nest depth increases. Both channels and chambers are located on the vertical projection of the entrance hole. Nests may reach a depth of up to 5.09 m, with a number of chambers ranging between 4 and 14.

Key words chambers, nest architecture, *Pheidole*, pitfall-trap
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Introduction

Pheidole is a hyperdiverse and cosmopolitan genus, with about 900 known species, and a total estimated number of 1 500 species, considering those that have not yet been described (Wilson, 2003). In Brazil, *Pheidole* is well represented and widely distributed across all regions. At least 27 species are known to occur in the state of São Paulo (Kempf, 1972). *Pheidole oxyops* occurs in cerrado (savanna) areas and on the edges of semideciduous forests. It has been reported to occur in Paraguay, northeastern Argentina, and in the states of Goiás, Mato Grosso, Minas Gerais, and São Paulo. According to Wilson (2003), this species belongs to the *diligens* group (86 known species), comprising exclusively predatory or scavenger species, without seed collectors.

The nest entrance of *Pheidole oxyops* is remarkable for its wide opening, acting as a pitfall-trap to capture live prey, supplementing the diet by foraging on dead or injured insects, which increases the importance of this species as a predator (Fowler, 1987). In soybean fields, other *Pheidole* species, such as *P. dentata*, *P. metallescens*, and *P. morrisi* feed on a large number of insects (Whitcomb *et al.*, 1972). Although *Pheidole oxyops* captures many insects (88.81%) (De Biasi, 1986), the number of live insects is very small (Bucher, 1974; De Biasi, 1986), but they can at times capture debilitated insects more than 5 m away from the colony (Fowler, 1987). This species is responsible for adult boll weevil (*Anthonomus grandis*) predation in cotton

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fields where their nests occur, accounting for up to 90% of predation (Fernandes *et al.*, 1994).

Pheidole nests have been studied previously, though little is known about their functional morphology and role in ecosystems. Bucher (1974) was the first to study the structure of *Pheidole* spp. nests in Latin America (Tucuman -Argentina). The author revealed that these colonies show a striking adaptation to life in arid environments. He also observed that nests have a wide entrance and chambers present vertical distribution, with depths of up to 6.60 m. The author adds that this type of nest is typical of the genus, in both predator and granivorous species. One species that presents molded nests is *Pheidole morrisi*; the nest also has a series of vertical chambers, but with an estimated depth of 55 cm and populations of up to 6 000 workers in adult nests (Tschinkel, 2003). This species belongs to the *fallax* group (Wilson, 2003), which is basically a predatory and scavenger group, with occasional collection of seeds, probably as a secondary source of food (Naves, 1985).

The genus *Pheidole* has a high population density at the cerrado in the Botucatu region, ranging from 0.24 to 1.22 colonies/m^2 (De Biasi, 1986). This genus has been little studied by researchers. Observations on the structure of its nests are exceedingly important to obtain knowledge about these ants.

The objective of this study was to contribute knowledge on *Pheidole oxyops*, by studying the structure of its nests using cement casting or neutral talc and subsequent excavations.

Materials and methods

Seven *Pheidole oxyops* nests were studied in the cerrado, at the Rubião Junior region, district of Botucatu, state of São Paulo, Brazil. Four colonies were excavated and marked with neutral talc, which was applied with a hand duster. Another three colonies were studied by casting, using cement.

Trenches (4 m^2) were opened for the colonies studied using neutral talc as marker. Each trench was parallel and on the side of the studied nest, with variable depth. Next, the talc was applied on the nest's main entrance and the nest was carefully excavated by removing the dirt until the talc-identified chambers and channels were reached.

The excavated channels and chambers were carefully cleaned for measuring. The structures were then numbered, sketched and photographed.

In order to observe the structure of the colonies using cement casting, three nests were previously prepared with a suspension consisting of 3 kg cement mixed with 10 L of water (Jacoby, 1935; Moreira *et al.*, 2004). The mixture was poured uninterruptedly into the nest entrance, thus preventing the formation of bubbles that appear due to cement contraction and water infiltration into the soil. Fifteen days later, as the cement became completely hardened, the ant nest was excavated using the above-described technique. The castings were carefully removed, especially those located in channels.

The castings were then transported to the laboratory and washed with a brush moistened in water and soap. The following measurements were obtained: nest entrance diameter, length and perimeter of the entrance channel, chamber height and diameter (larger and smaller), channel length and width, total depth of excavated nests, and number of chambers. The structures cast in cement were measured, photographed, and drawn on a 1:7.5 scale, as well as on their life size.

Results

The *Pheidole oxyops* colonies have a wide, irregularly shaped nest entrance, whose diameter varies from 5.09 to 12.20 cm (Table 1). The entrance channel is cylindrical, with a mean length of 13.55 cm and irregular formations. The channel diameter becomes progressively narrower until the nest's first chamber appears (Fig. 1).

After the first chamber comes the first channel, which is very wide and short, a little smaller in width than the chamber (Fig. 1). The initial chambers are very close together, separated by just a short and wide channel. The number of chambers varied from 4 to 14 among the studied nests, vertically distributed through a depth from 101−509 cm

Table 1 Nest entrance diameter measurements (cm) for entrance-channel length, number of chambers, and total depth of colonies in seven nests of *Pheidole oxyops*.

	Mean	Standard deviation	Maximum	Minimum
Entrance diameter	9.35	2.86	12.20	5.09
Entrance-channel length	13.55	3.24	20.00	10.00
Number of chambers	8.14	3.33	14.00	4.00
Total depth of colonies (total length)	223.77	154.49	509.00	101.00

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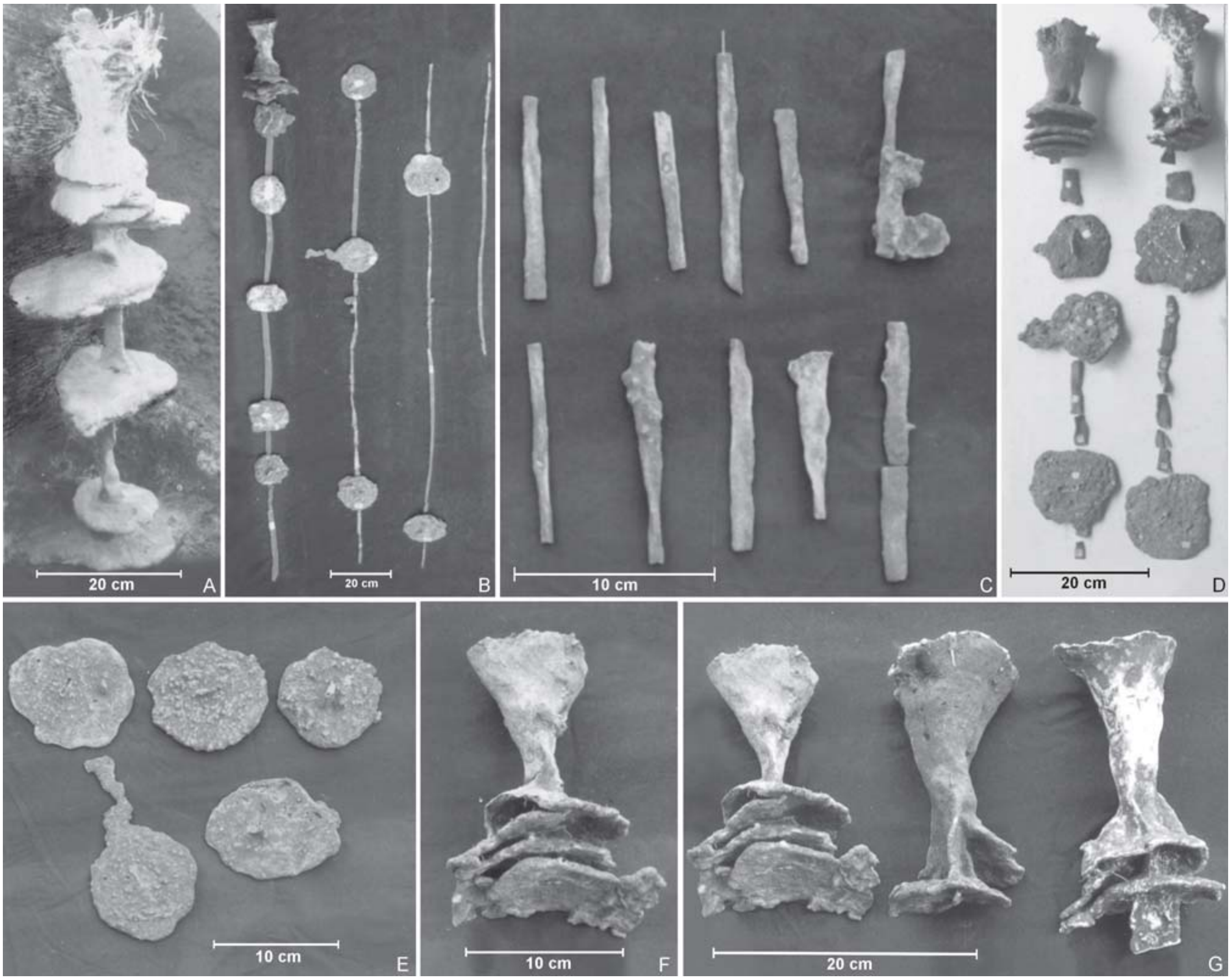

Fig. 1 Architecture of *Pheidole oxyops* nests cast in cement: general view of the nest (A), nest structures (B and D), channels that connent chambers (C), chambers (E), and entrance channel (pitfall-trap) and first chambers (F and G).

(Table 1). Beyond the initial set of chambers, the channels that interconnect them become progressively narrower and longer and the chambers are separated by greater distances (Figs. 1−3).

The chambers are flattened, varying in diameter, and present irregularly-shaped edges (Fig. 1). They are slightly convex on the top and concave on the bottom. Chamber thickness, and the largest and smallest nest diameter values of *Pheidole oxyops* cast cement nests can be seen in Table 2, as well as the diameters of colonies excavated using neutral talc.

Sometimes, small chambers used as refuse deposits can be found on the side of the main chambers. Pairs of close-by chambers can also be found, separated by a channel of only 0.6 cm in length.

The channels depart from the center of the chambers, and are wider toward the upper part of the chambers and narrower on the bottom, just below them (Fig. 1). The channels may present enlarged portions like those observed in the nests, and may also switch their position completely, in turns of 90° or less. Channel width varied greatly among the sampled channels (Table 3). Both channels and chambers are located on the vertical projection of the nest entrance.

Table 2 Diameter (cm) of *Pheidole oxyops* chambers using neutral talc labeling and cement casting.

	Measurements	Mean ± SD	*n*
Cement	Largest diameter	13.52 ± 2.66	26
	Smallest diameter	12.01 ± 2.16	26
	Thickness	0.71 ± 0.17	22
Neutral talc	Diameter	12.53 ± 3.89	30

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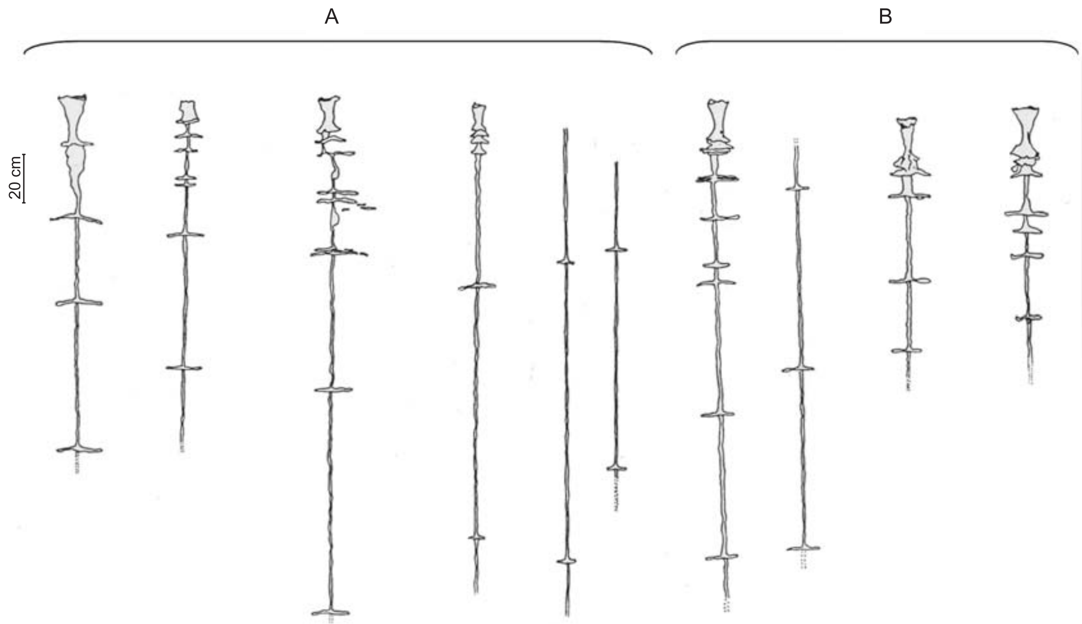

Fig. 2 Architecture of seven *Pheidole oxyops* nests, sketched form excavations marked with neutral talc (A) or cast in cement (B). Scale: 1:7.5.

Table 3 Channel width (cm) of *Pheidole oxyops* colonies cast in cement at various locations.

Location	Mean ± SD	*n*
1 cm below the preceding region	1.98 ± 0.85	13
Middle region	3.78 ± 3.14	19
1 cm of the subsequent region	2.73 ± 1.52	12

Discussion

Pheidole oxyops has subterranean nests, with a distinctive and easily recognizable external architecture, with a wide and specific entrance hole, denoting a pitfall-trap. Bucher (1974) verified that the entrance hole of *Pheidole oxyops* nests is shaped as an irregular, easily recognizable funnel, with a maximum width of 20 cm and depth from 25−30 cm. Our observations match those by Bucher (1974) with regard to the shape of the entrance hole, but differ with respect to width and depth, since we found a maximum width of 12 cm, while depth varied from 10−20 cm. In addition, this depth is essential for the entrance hole to function as a pitfall-trap, because it is directly correlated with the surface area of the nest's entrance hole, which prevents the prey from escaping (Fowler, 1987). The nest has a large-diameter entrance, oscillating between 5.09−12.20 cm, and a wide entrance hole becomes progressively narrower until ending up as irregular dilatations, with chambers very closely arranged together, finally transforming into a broad central channel (Table 3). Such large openings significantly facilitate a great flow of ants, since the diet consists of large, whole adult insects, insect parts, young individuals, and exuviae, totaling 88.81% (De Biasi, 1986). These insects are hunted and transported in groups, allowing the ants to enter their nests with very large prey items, weighing up to 19.0 mg. As soon as the ants arrive inside the nest, they are free from competition.

The external aspect of the nest (external architecture) has been used earlier to separate nesting forms in ants by Wheeler and Wheeler (1976). The authors noticed that some species have a single entrance surrounded by the crater. This is common in the genera *Conomyrma*, *Forelius*, *Lasius*, *Manica*, *Myrmecocystus*, *Paratrechina*, *Pheidole*, and *Veromessor*. The craters are dirt mounds made by the workers and are found in grasslands, forest openings, deserts, and in all disturbed habitats. In *P. oxyops*, during the rainy season in Brazil, the ants frequently form a ridge of excavated soil that surrounds the nest structure, probably to reduce rainfall run-off into the nest (Fowler, 1987).

The number of chambers in *Pheidole oxyops* is small and variable (the maximum number observed is 14) with diameters ranging from 8−21 cm, and widths from 0.4−1.1 cm. Bucher (1974) verified that *Pheidole oxyops* chambers are flat and 12 cm in diameter, with a 3 cm height. Our data match those of Bucher with regard to chamber shape, but differ with regard to size, since we observed diameters ranging from 8−21 cm. In this work, we verified that the

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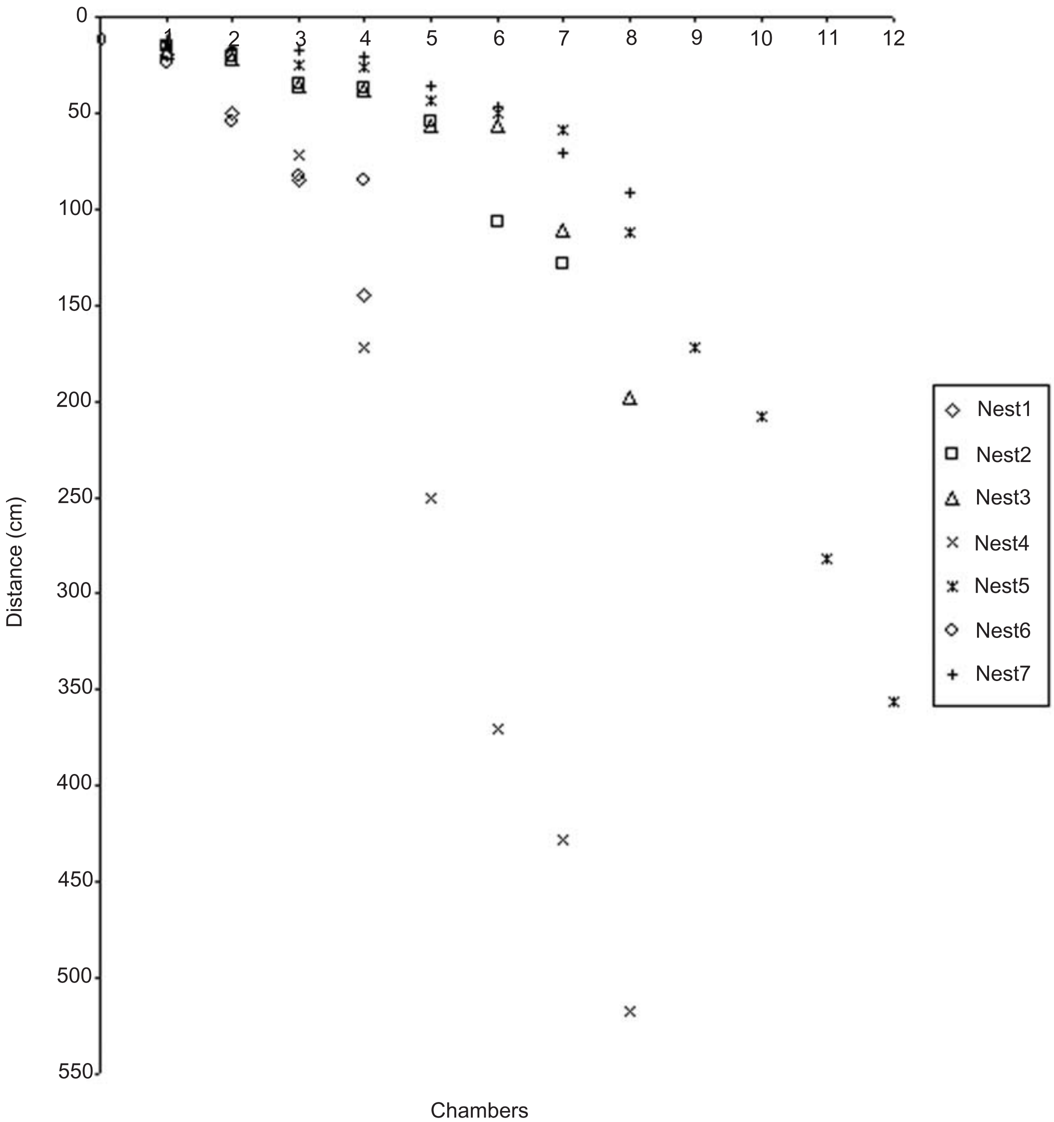

Fig. 3 Distance between chambers (cm) in seven *Pheidole oxyops* nests.

chambers are located on the vertical projection of the colony's entrance, as similarly observed by Bucher (1974). This vertical structuring of the nests is due to the fact that workers excavate according to their spatial orientation, that is, workers organize themselves vertically within the nest according to worker age, developmental stage, and season of the year, probably following temperature and CO_2 concentration gradients (Tschinkel, 2006). In *Pogonomyrmex badius*, the harvester ant, it was verified that older workers are found in nest chambers near the surface, while younger individuals are found at greater depths (Tschinkel, 1999). According to the author, young, newly-emerged workers move in an ascending flow as they become older, that is, they leave the region where the brood is concentrated, and where they play an important nursing role, to develop other activities, including nest excavation, resulting in greater development of superficial structures. When they appear at the surface, they switch to guarding and foraging, creating an age polyethism pattern. Probably, *P. oxyops* follows a similar pattern as the one found in *Pogonomyrmex badius* because, in addition to the vertical distribution of channels and chambers, the ants are present in higher numbers at the superficial regions, where the interconnecting channels become progressively narrower and longer and the chambers are spaced at greater distances from each other.

Recently, it has been verified that this social stratification follows a CO_2 gradient. Tschinkel (2004) experimentally demonstrated that younger workers prefer high CO_2 concentrations, and thus are found at deeper regions of the nest, where concentrations of this gas are five times as high as at the surface. In addition, workers show a greater tendency to excavate at low concentrations, found near the soil surface, which is the place where workers that are more skilled at excavating (older workers) can be found.

Although it is not known how worker and brood distribution occurs inside *Pheidole oxyops* nests, and by which mechanisms such distribution takes place, it can be inferred that internal architecture is a reflex of the workers' digging behavior and nest microclimatic conditions. In our study, *Pheidole oxyops* workers produced nests up to 5.09 m in depth, similar to those found by Bucher (1974), with chambers at depths of up to 6.60 m. Another important observation made in our study concerned the interconnection between lateral chambers and the main chambers. The former are used as refuse deposits, and are very reduced in size, smaller than the main chambers. A good example of chamber differentiation for specific purposes is found in the grass leaf-cutting ant, *Atta capiguara*. This species builds huge refuse chambers, morphologically differentiated from those used to grow the symbiotic fungus (Forti, 1985).

With regard to the structure of *Pheidole oxyops* colonies, it was concluded that they have a vertical projection, with a higher number of chambers at smaller depths. In addition, channel length increases with depth.

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