5668

Ins. Soc. *40*:301–311 (1993)

1015-1621/93/030301-11 $ 1.50 + 0.20/0

Biology and myriapod egg predation by the Neotropical myrmicine ant *Stegomyrmex vizottoi* (Hymenoptera: Formicidae) *

J. L. M. Diniz and C. R. F. Brandão

Museu de Zoologia da Universidade de São Paulo, C.P. 7172, São Paulo, SP, 01064, Brasil

Key words: Ant, *Stegomyrmex*, egg predation, myriapod, Neotropical, Formicidae, Hymenoptera.

Summary

For the first time for a Neotropical ant and for Myrmicinae, the searching behavior and specialized predation of spirobolid millipede eggs by *Stegomyrmex vizottoi* Diniz will be described. The relationship between morphology and habits is studied, as are nest architecture and distribution of the ant population in the nest chambers. We also report on some observations of behavior in the field and laboratory.

Introduction

There are several published observations of ants preying on arthropod eggs, although most accounts are of generalists' diets. Some ants are, however, specialized to some degree in preying on arthropod eggs.

Eidmann (1936) found many globular objects resembling arthropod eggs inside natural nest chambers of *Erebomyrma eidmanni*, while Brown (1979) and Wilson (1962) found similar structures piled along with the troglophilic *Erebomyrma urichi* brood in natural nests. Wilson (op. cit) stated that those eggs "were cared for by the captive colony in the artifical nest and may have been used sporadically for food, although direct feeding was not observed".

Hölldobler and Wilson (1990) considered *Erebomyrma* as the least-specialized oophagous genus, as they readily accept freshly crushed larvae and pupae of *Tenebrio molitor*, as well as chopped *Armitermes* and moths. This genus has also been fed moth eggs in the laboratory (see Wilson, 1986, for *E. nevermanni*).

Solenopsis laeviceps was observed by Emerson (in Wheeler, 1936) to nest at the bottom of termite nests at Kartabo, Guyana, where he once found 75 to 100 termite

---

* We dedicate this paper to William L. Brown Junior, on the occasion of his 70th birthday.

B

eggs in the ants' chambers. In another nest he observed that the ants had stored many termite eggs and a single Staphylinidae (termitophilous) egg among their larvae.

The most specialized oophagous ant species are known to belong to the Ponerinae. In *Proceratium* (Ectatommini), at least four species have been observed storing and feeding on spider eggs and, rarely, on other arthropod eggs (Brown, 1957, 1958, 1974, 1979). The related minute ectatommine *Discothyrea* also collects, stores, and feeds on arthropod eggs, probably of spiders and centipedes (Brown, 1979; Lévieux, 1972, 1982, 1983). The ponerine *Plectroctena lygaria*, from West Africa, stores in its nest large numbers of millipede eggs, which appear to constitute their exclusive diet (Bolton et al., 1976). The data of *P. subterranea*, feeding likewise on diplopod eggs (Lévieux, 1972, 1983), may also refer to *P. lygaria* (Bolton et al., op. cit.).

Brown (1979) considered the information available in the literature on arthropod egg predation by ants not at all exhaustive. In the case of *Plectroctena* he said that adults of the large species are also predators of adult millipedes (see also Dejean and Suzzoni, 1990 and Villet, 1991). The Neotropical *Thaumatomyrmex contumax* also captures and preys on adult polyxenid millipedes. However, before eating them, the ants remove the millipedes' cover of setae, that probably release an aversive substance (Brandão et al., 1991).

Stegomyrmex ants are considered extremely rare. In museums one can find less than fifty individuals collected from very few localities, and nothing is known about their biology. The genus is the sole representative of the Neotropical tribe Stegomyrmecini, and has been recently revised by Diniz (1990), who studied all specimens known to be kept in museums. He recognized three species: *S. manni* Smith from Panama, *S. connectens* Emery from Peru and Bolivia, and *S. vizottoi* Diniz from Southeastern Brazil and Paraguay. Lenko (1965) found a worker of the latter species (although identified as *S. manni*) in the gizzard of *Conopophaga lineata* (Aves, Formicariidae). Diniz (op. cit.) found three workers of *S. vizottoi* in a small chamber under a plant vase, with no traces of construction. Hölldobler and Wilson (1986) described the coating of *S. connectens* integument (identified by them as *S. manni*) with a thin muddy layer of dirt, greatly enhancing the overall camouflage of the body. They also observed a similar coating in relatively old workers of basicerotine ants (Myrmicinae).

For the first time for the Neotropics and for the Myrmicinae, the searching behavior and specialized predation of myriapod eggs by *Stegomyrmex vizottoi* are described. The reasons why we believe that this represents a very specialized behavior are discussed below. We studied the morphological features related to *S. vizottoi* habits, and describe nest architecture, distribution of its population within chambers in natural nests, and comment on some other observations of its behavior in the field and in the laboratory.

Morphology

The *Stegomyrmex* antennal carinae are much enlarged, forming lobes that completely cover the deep and elongate antennal scrobes, into which the ants can entirely

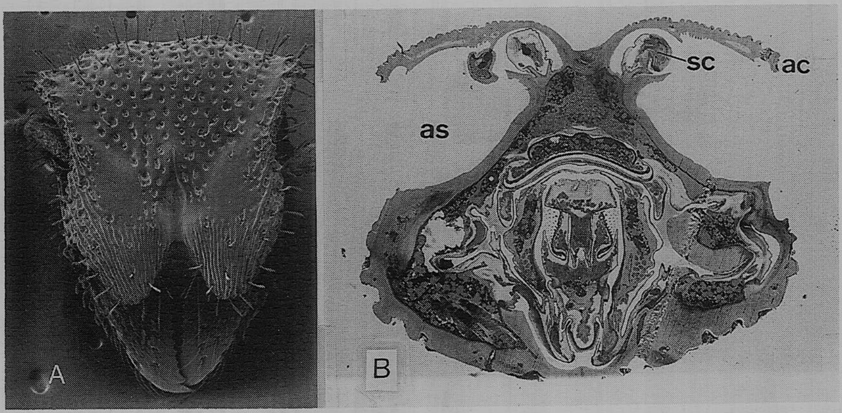

Figure 1. Heads of *Stegomyrmex vizottoi* workers from Mirassol, São Paulo state, Brasil. A) Full-face view. Note the foveolae, rugulae, and clubbed hairs. The flexible hairs at the clypeus and mandibles are not employed in earth-capturing. B) Transverse section of the anterior portion showing the greatly enlarged lobes of the antennal carinae (ac), scrobe (as), and base of scape (sc). Head width across eyes = 1 mm

conceal the antennae (Fig. 1). In addition to accomodating the antennae, the expanded antennal carinae provide a shield for the compound eyes, suggesting cryptic habits. Eye defense is enhanced when the antenae are withdrawn (Fig. 2). The scrobe is not limited ventrally by a carina.

This situation is totally different from the one found in the Basicerotini and Attini, tribes traditionally considered close to the Stegomyrmecini. In these tribes the compound eyes are always fully exposed, although in some genera the exposure corresponds to a notch at the frontal lobes. Furthermore, in *Basiceros*, the genus considered the most generalized living basicerotine, the antennal fossae, where the base of the scape articulates, are distinct from the scrobe, which accomodates only the funiculus. The eyes are placed on the edge of the antennal carina, above the scrobe, and are protected by the greatly expanded scapes when they are held against the sides of the head. In the Attini, although the position of the compound eyes is similar to that in *Stegomyrmex*, the scrobes can even surpass the vertex and are limited ventrally by a conspicuous carina, sometimes interrupted at eye level.

Hölldobler and Wilson (1986) described the differences in types of hairs between *Basiceros* and *Stegomyrmex*. *S. vizottoi* presents (Fig. 2), as a diagnostic pattern of the species (Diniz, 1990), only clubbed hairs on the dorsum of the head and pronotal disc, but there are some wire-shaped holding hairs on the prosternum and on the ventral face of postpetiole. Brush hairs are found exclusively in fringes on the posterolateral corners of the head and on the lateral margins of the pronotum.

Foraging

In daylight we recently collected stray workers of *S. vizottoi* foraging alone under logs deposited in an urban area in Mirassol, state of São Paulo, Brazil. They seemed to

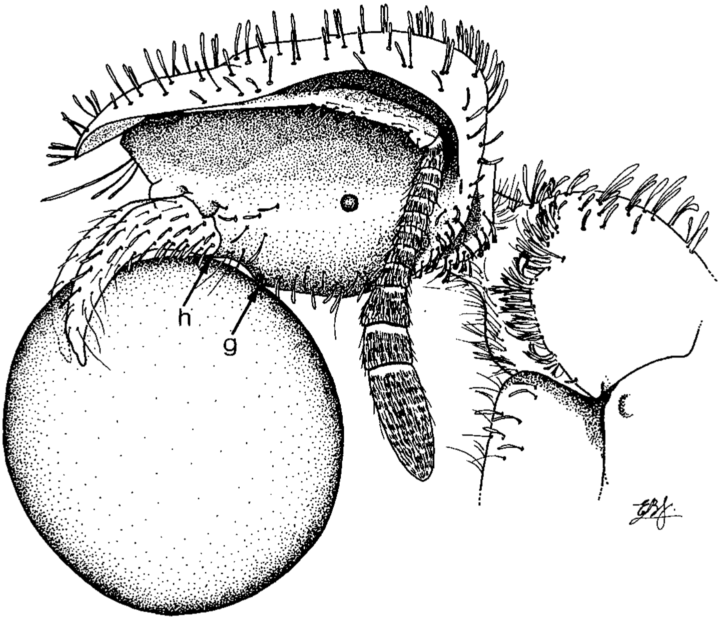

Figure 2. Lateral view of head and anterior portion of trunk, showing the antennal scrobes and diplopod egg being held under the mandibles. Note the curved mandibles acting as pincers, the two points at the anteroventral region of head, indicated by arrows – hypostomal (h) and anterior gular (g) regions – that help to support the egg, and the head-pronotal fringe of brush hairs

avoid light, walking preferably under leaves or searching small crevices. To observe them walking above ground, it was necessary to shade the area with an umbrella.

The workers walked very slowly, inspecting every small opening, fissure, or cleft in the soil. We wondered whether they were searching for their nest, but then we noted one particular ant excavating the soil inside such a cavity, working it with the mandibles into small pieces, and forcing back the small blocks with its forelegs. While working, it completely withdrew the antennae (scape and funiculus) into the scrobes. After some minutes the worker, with one half of its body already in the cavity, left the opening, carrying an egg under the mandibles. Following this and other individuals searching for eggs, we observed that sometimes workers could even disappear in cavities for many minutes, perhaps exploring or inspecting natural chambers or tunnels. During this process, repeated many times in daily foraging trips, the workers gradually accumulated soil particles on their bodies, becoming covered with a muddy sheet, which seemed to act as a protective shield and as camouflage. As pointed out by Hölldobler and Wilson (1986), and as can be seen in Fig. 1a, their integument is foveolate, and can accrete earth with the aid of specialized hairs. Adding this effect to the slow movements and to the habit of feigning death almost immediately after any disturbance, we have realized why these ants are so rarely collected.

Although most field observations were made in daylight, some workers were also observed foraging at night, between 8 and 10 PM. We also noticed that foraging workers can stay out of the nest for more that one day. This observation may be related to that by Diniz (1990) of a small chamber with three workers that apparently was not part of a nest, but could possibly be housing foraging individuals during an extended trip.

The workers hold the prey eggs below the ventral faces of the mandibles, which are curved in such a way as to provide, along with the hypostomal and anterior gular regions, four points for holding the egg (Fig. 2). The mandibles are thus used to apply pressure and not as pincers or forceps. Even when disturbed the carrier ant never releases the egg.

We followed the first egg-carrying worker and found a nest opening; in fact, this was the very first *Stegomyrmex* nest ever found. We did not excavate the nest, leaving it alone for further studies, but observed that the opening was circular, 2 mm in width. There was no loose earth around the opening, nor any other observable mark. We also noticed three other workers leaving the nest entrance for the foraging area.

We collected the first worker and its egg and brought them to the laboratory, but did not succeed in rearing the egg. We also collected the soil around the foraging area and swept it, obtaining three eggs similar to the ones found with the ants, probably eggs of gastropods or some small arthropods. Unfortunately, this area has been severely disturbed since and we have never been able to find this nest entrance again. We do not know whether the ants moved it.

Months later (January, 1990), however, we found in a similar situation another foraging worker in the same area. We again provided shade and observed the ant entering a natural opening in the soil. As the environment was too complex for observation, we removed the litter, consisting of fresh and dead leaves, twigs, small stones, etc., from the surrounding area. It seemed that this procedure helped to reveal eggs, because moments after we cleared the surface, eight workers came out to forage in the area, enabling us to find another nest entrance, on an inclined surface and also with a diameter of 2 mm.

Aggressive encounters were observed many times among foraging workers, suggesting colony recognition.

In order to learn which animal was responsible for the eggs found with the ant workers, we collected the superficial soil and divided it over three plastic boxes (20 × 15 × 10 cm) after sterilization at 200 °C. In one box we added all diplopods previously found the soil, in another we added the subulid gastropods, and in the last one the arachnids and Dermaptera. Some months later we swept the soil in the boxes and collected all eggs laid.

We found that the eggs carried by the ants were identical to those laid by the spirobolid diplopods. We then kept the millipedes in the same box to obtain more eggs to feed the ants in the laboratory. There the diplopods buried themselves, while in the field we have encountered them only under rocks or logs, inside logs partially filled with earth, buried in the leaf mold, in crevices under bark, or even under lumps of soil. While sweeping the ground or looking for *Stegomyrmex* ants in the field, we noticed that myriapod eggs are mostly found with a protecting soil "cocoon" (Fig. 3), that acts as an earthen nest, sometimes rather complicated; the soil grains and excrements are possibly held together by the products of the specialized anal glands of myriapods. Smaller eggs were found near the surface, while larger ones were found up

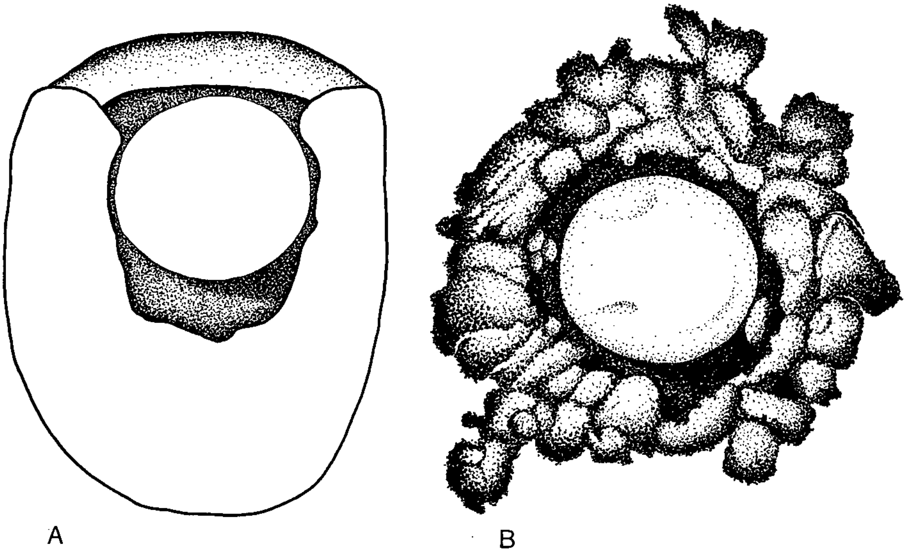

Figure 3. Diplopod eggs as found in the field. A) Diagram of slide of egg covered by earth coccon (cap removed). B) Drawing of the same from above

to 40 cm deep in the soil. Although we did not measure the distances between eggs, their distribution in the area we studied seemed rather clustered.

Nest architecture

Opening the second nest found we were able to confirm that there was no other entrance to the first chamber (Fig. 4). The sinuous tunnel leading to this chamber had a diameter of 3–4 mm and a length of *circa* 40 cm. We observed along the tunnel three irregular expansions, up to 10 mm high, and many dead ends. The tunnel reached the first chamber at one of its corners. This chamber housed only workers, had an irregular floor, and measured 67 × 10.5 × 10 mm. In the corner opposite the entrance there was a pile of refuse, mainly diplopod egg shells. Near the center of the first chamber roof, we noticed a funnel-like structure 10 mm long, acting as an opening to the main chamber above. This funnel seemed to have been constructed by the workers and was almost 10 mm in diameter below, 2 mm at its upper end. We observed that the funnel is placed in such a way that to gain access to the main chamber a worker would have to walk upside down on the chamber roof and then “climb” the funnel outer border. The main chamber, with a much more regular pavement, housed the queen, all the immatures (10 ant eggs and 50 larvae) and workers. We found no prey eggs within the chambers. The total worker population of this colony (hereafter called Colony 1) was 76.

Anísio M. Diniz collected part of another colony (Colony 2) in the same area, in January 1991, and found a single chamber 7 × 4 cm, within a brick wall at a depth of

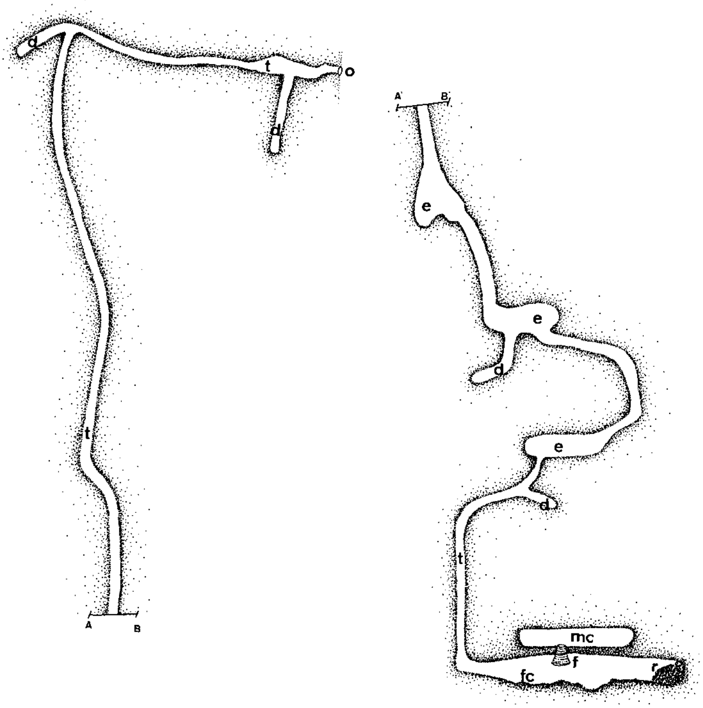

Figure 4. Sectioned diagram of a natural nest of *S. vizottoi*. Opening (o) to an inclined earth surface, expansions (e), dead ends (d), tunnels (t), first chamber (fc), funnel (f), refuse (r), and main chamber (mc). See text for the measurements

about 30 cm. There he found, in separate groups, 22 winged and 7 wingless females, immatures in all stages and a pile of 169 "small round white balls", besides about 300 workers. These eggs, although homogeneous in size and color, were much larger than the ones found in the first nest. The collector described the ants as moving very slowly, even when disturbed.

Both colonies were brought to the museum laboratory and transferred to two similar artificial gypsum nests; an attempt to reproduce the natural nest architecture, although horizontally developed.

Colony 1 workers constructed a funnel linking the chambers, quite similar to the one we found in natural conditions. We let a diplopod enter the first chamber, where it remained for days, never succeeding in entering the chamber of the queen and immatures. The workers in the first chamber tried many times to push it back, using their flattened heads as shields. Some *Collembola* once entered the artificial nest from the earth box, and reached the first chamber, where they fed on the refuse, but never succeeded in entering the main chamber. We believe then that the funnel has a defensive function, excluding soil arthropods.

Prey preferences and feeding

In the artificial nest arenas we offered eggs and nymphs of Dermaptera, eggs of beetles (Tenebrionidae, Lagriinae), of diplopods, earthworms, and gastropods, Tenebrionid larvae, termite workers, live and dead Collembola, dead Diptera, pieces of nuts, honey/water (1:1), sugar/water, pieces of sardine, raw meat, and cooked and fresh hen egg yolk. Workers seemed to concentrate around the meat, but only carried gastropod and diplopod eggs back to the nest. Eggs of apparently several species of diplopods were readily collected by nestmates, while those of the gastropods were abandoned within the chamber. Since it seemed that the ants were unable to open the gastropod egg chorion, we split them, but even then the ants did not eat the contents.

When offering diplopod eggs at the arenas we covered them with humid soil and small twigs. After some time, a foraging worker, exploring the arena surface, would concentrate on the spot were we had buried an egg, touched the place many times with the antennal tips, removed the earth, and then took the egg. We never saw them carrying twigs or pieces of earth which blocked their way to the egg, but they always pushed them back with their heads, assuming a characteristic position of the legs and trunk.

The first worker to find an egg would go back to the tunnel as far as the first chamber and holding the egg in the way described, always excitedly scratch the nest floor with the gaster apex. Other workers would then go out to forage in the arena. When encountering a carrier, the newly recruited workers try to "steal" the egg. This is especially true after a starvation period. Also in such periods the workers can spoil an egg while carrying it, and eat it before reaching the pile. The carrier worker "protects" the egg from being taken by another worker by lowering its head and keeping the antennae fully concealed within the scrobes. When strongly "attacked", these ants can start eating the egg before reaching the first chamber.

An egg is deposited in a pile at the main chamber only after one or more workers have actively cleaned every particle of dirt from it with their mouthparts. We wondered whether this procedure, which always occurs in the first chamber or in the expansions along the tunnel, would also clean adventitious bacteria and fungi from the eggs. The pile assembled by Colony 1 was kept beside the ants' immature pile, and included diplopod eggs of different sizes and colors, varying from white to light yellow, showing that the ants accept as prey the eggs of several diplopod species.

Incidentally, we had observed previously that other myrmicine species of *Solenopsis* and *Pheidole* also carry diplopod eggs, but only when found naturally free from their earth covering.

The pile of diplopod eggs in the main chamber, which is probably accumulated for regular feeding, but specially during the dry and cold seasons, grows continually throughout the wetter months. The workers can take one egg from the pile for feeding alone or share the egg with up to five nestmates. From January to July, 1990, Colony 1 collected 1091 eggs in our arena, all the eggs we offered.

One egg is taken from the pile at a time. Some may be offered intact to the larvae, at the larval anterior ventral region. The larvae will then break the chorion and eat the egg contents. We observed instances when the queen and/or workers shared the prey egg with the larvae. Queens are, incidentally, much harder to observe, as they are more sensitive to light than the workers. They reacted violently every time we illuminated the main chamber for observation.

Colony population

The population of Colony 1 grew, from January 1990 (collecting date) to July 1990, from 76 to 123 workers. We were also able to follow the immature population. Their number grew to a peak around March. An egg takes 28–30 days to hatch, the larvae 34–36 days to pupate, and the pupae 25–27 days to eclose. Callow workers remain inside the chambers for about 10 months prior to foraging in the arena.

In April the queen discontinued egg-laying. By mid-May there was a shortage of diplopod eggs, as we were not able to find them in the field or in our rearing boxes, and the ant workers started to cannibalize their own larvae and pupae. In July we found no immatures and the nest entrance was kept closed with a plug of earth previously carried to the first chamber. After this, the ants closed also the tunnel leading to this chamber in several places. We believe that in the field the nest may be closed with a plug as well, because we marked the first nest found, but could never find it again. The workers then piled themselves in the main chamber, where they spent the winter. At the beginning of October the workers cleaned the tunnel and opened the nest entrance. In fact, we never collected *Stegomyrmex* between July and October.

We kept Colony 1 from January 1990 to July 1991, observing two peaks of egg production between October and July, the first around November and the second around February. In the second season the ants again collected all diplopod eggs offered at the arena (2679 eggs). Although the worker population reached 193 at the end of the second season, we believe that it was still immature, as it never produced sexuals. Summing up our observations in artificial nests with data found on labels on museum specimens, we believe that alates fly from February to April, differing from most ant species in south eastern Brazil, which release sexuals from October to January.

Discussion

Although we studied live colonies of only one of the three known species of *Stegomyrmex*, the similar sculpturing and pilosity patterns and the presence of a conspicuous modification of the gular region in all species (see Figures in Diniz, 1990 and Fig. 2), lead us to hypothesize that the habits we have described for *S. vizottoi* are common to all *Stegomyrmex*.

Colony 2, which was evidently mature when collected, was collected only in part and had more than 300 workers and several alate and apparent recently dealated queens. Thus our data suggest that a colony reaches maturity after producing some 300–400 workers.

Our observations indicate that millipedes do not lay eggs year round, but concentrate oviposition from October to April, corresponding to the wet season in southeastern Brasil. All foraging *Stegomyrmex* workers found up to now have been seen collecting during this period, which we have called the favorable season.

Acknowledgements

We would like to thank Johan Billen for this expertize, the preparations, and photographs in Figures 1 a and 1 b. Anísio M. Diniz and Adelino D. da Silveira helped in the field. Bodo Dietz translated the German reference. Eliana M. Cancello, Flávia Ejchel, Márcia F. L. Françoso, Miriam D. Marques, Ricardo V. S. Paiva, Adriana R. Menezes, and specially P. E. Vanzolini critically read the manuscript. Claudio M. Martins identified the gastropods. CNPq, CAPES and FAPESP supported our work.

References

Bolton, B., W. H. Gotwald and J.-M. Leroux, 1976. A new West African ant of the genus *Plectroctena* with ecological notes (Hymenoptera: Formicidae). *Ann. Univ. Abidjan sér. E (Ecologie) 9*:371–381.

Brandão, C. R. F., J. L. M. Diniz and E. M. Tomotake, 1991. *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Ins. Soc. 38*:335–344.

Brown Jr., W. L., 1957. Predation of arthropod eggs by the ant genera *Proceratium* and *Discothyrea*. *Psyche 64*(3):115.

Brown Jr., W. L., 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). *Bull. Mus. Comp. Zool. Harvard 118*(5):175–362.

Brown Jr., W. L., 1974. A remarkable new island isolate in the ant genus *Proceratium* (Hymenoptera: Formicidae). *Psyche 81*(1):70–83.

Brown Jr., W. L., 1979. A remarkable new species of *Proceratium*, with dietary and other notes on the genus (Hymenoptera: Formicidae). *Psyche 86*(4):337–346.

Dejean, A. and J. P. Suzzoni, 1990. Monomorphism and polymorphism in African Ponerinae with a specialized alimentary diet: does this have any bearing on the type of prey? In: Veeresh, G. K., B. Mallik and C. A. Viraktamath (eds.) *Social Insects and the Environment.* Proc. 11th Int Congr. IUSSI, Bangalore. New Delhi, Oxford & IBH Publ. Co. Ltd, p. 339.

Diniz, J. L. M., 1990. Revisão sistemática da tribo Stegomyrmicini, com a descricão de uma nova espécie (Hymenoptera, Formicidae). *Revta bras. Ent. 34*(2):277–295.

Eidmann, H., 1936. Oekologisch-faunistische Studien an südbrasilianischen Ameisen. *Arbeit. phys. angew. Ent. Berlin-Dahlen 3*(1):26–48, 81–114.

Hölldobler, B. and E. O. Wilson, 1986. Soil-binding pilosity and camouflage in ants of the tribes Basicerotini and Stegomyrmecini (Hymenoptera, Formicidae). *Zoomorphology 106*:12–20.

Hölldobler, B. and E. O. Wilson, 1990. *The Ants.* Cambridge, Belknap Press of the Harvard Univ. Press, 732 p.

Lenko, K., 1965. Sôbre a ocorrência de *Stegomyrmex manni* no Estado de S. Paulo, Brasil (Hymenoptera: Formicidae). *Studia ent. 8*:201–204.

Lévieux, J., 1972. Le role des fourmis dans les réseaux trophiques d'une savane préforestière de Cote-d'Ivoire. *Ann. Univ. Abidjan ser. E (Ecologie) 5*(1):143–240.

Lévieux, J., 1982. A comparison of the ground dwelling ant populations between a Guinea savanna and an evergreen rain forest of the Ivory Coast. In: Breed, M. D., Michener, C. D. & Evans, H. E. (eds.) *The Biology of Social Insects.* Proc. 9th Int Congr. IUSSI, Boulder, Colorado, Westview Press, p. 48–53.

Lévieux, J., 1983. The soil fauna of tropical savannas, IV: The Ants. In: Bourlière, F., (ed.) *Ecosystems of the World. 13. Tropical Savannas*, Amsterdam, Elsevier Scient. Publ. Co., p. 525–540.

Villet, M. H., 1991. Colony founding in *Plectroctena mandibularis* F. Smith, and the evolution of ergatoid queens in *Plectroctena* (Hymenoptera: Formicidae). *J. Nat. Hist. 25*:979–983.

Wheeler, W. M., 1936. Ecological relations of Ponerinae and other ants to termites. *Proc. Am. Acad. Arts Sci.* *71*(3):159–243.

Wilson, E. O., 1962. The Trinidad cave ant *Erebomyrma* (= *Spelaeomyrmex*) *urichi* (Wheeler), with a comment on cavernicolous ants in general. *Psyche* *69*(2):62–72.

Wilson, E. O., 1986. Caste and division of labor in *Erebomyrma*, a genus of dimorphic ants (Hymenoptera: Formicidae: Myrmicinae). *Ins. Soc.* *33*(1):59–69.

Received 5 May 1992;
revised 20 October 1992;
accepted 18 November 1992.