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"Wall-papering" and elaborate nest architecture in the ponerine ant *Harpegnathos saltator*

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Summary

Excavation of 18 nests of *Harpegnathos saltator* from southern India revealed an unusually complex architecture for a ponerine ant. The inhabited chambers are not deep in the ground. The uppermost chamber is protected by a thick vaulted roof, on the outside of which is an intervening space serving as isolation from the surrounding soil. In large colonies, the vaulted roof is extended into a shell which encloses several superimposed chambers. Little openings, which may be encircled by moulded flanges, occur in the upper region of the shell. The inside of the chambers is partly or completely lined with strips of empty cocoons. A refuse chamber is always found deeper than the inhabited chambers; live dipteran larvae (family Milichiidae) are typically present. These elaborate nests represent a large energetic investment, and we speculate therefore that nest emigration is unlikely in this species. Consequently, colony fission may never occur, unlike other ants where gamergates reproduce.

Introduction

The Asian ponerine ant genus *Harpegnathos* is represented by only two species: *H. saltator* in southern India, and *H. venator* in northern India and Southeast Asia (including the Philippines and Hong Kong). *Harpegnathos* workers hunt solitarily and use their sting to paralyze and preserve their insect prey (Maschwitz et al., 1979). They frequently jump while hunting or escaping, being one of the few ant species capable of this (Wheeler, 1922; Maschwitz, 1981 a; Musthak Ali et al., 1992). The social organization of *H. saltator* is remarkably complex. In several colonies we found a single reproducing queen, but there can also be gamergates (mated egg-laying workers) whose reproduction is regulated by complex dominance interactions, including the most stereotyped antagonistic displays yet observed in ants (Peeters et al., unpublished). In the course of collecting the nests of *H. saltator*, we discovered that their architecture is often very elaborate. As Maschwitz (1981 a) already noted, these nests are exceptional among ponerine ants, which usually have simple nests. Here we describe their main features, and discuss the association between the existence of labour-expensive nests and the likelihood of colony emigration and eventual fission.

Material

Nineteen colonies of *Harpegnathos saltator* were excavated from four localities in Karnataka State, southern India: (i) Jog Falls, Uttara Kanada district – in March 1981 (1 nest), in October 1991 (3 nests), in May 1992 (6 nests), and in June 1993 (3 nests); (ii) campus of the University of Agricultural Sciences (G. K. V. K.) at Bangalore – 4 nests in October 1991; (iii) Bannerghatta Park near Bangalore – 1 nest in June 1993; (iv) Mudigere, Chikmagular district – 1 nest in March 1981. Whenever possible we dug a deep trench some distance in front of the nest entrance, and then proceeded laterally – this enabled us to study the vertical profile without damaging the roof. Some of the nests were measured and sketched in the field, while pieces of chamber walls were later examined with a scanning electron microscope.

Results

The nests of *H. saltator* occur close to the soil surface (top regions are only 120–250 mm deep). A variable number of elegantly constructed chambers are stacked directly on top of one another (Fig. 1). The chambers have flat floors, and their walls curve up to low, vaulted ceilings. We found considerable variability in the size of the nests, which probably corresponds to different stages in nest ontogeny. Some nests consisted of only one chamber, while larger nests (N = 7) had up to six levels of chambers.

A characteristic feature is the occurrence of a thick vaulted roof protecting the uppermost chamber. It is conspicuous because a gap 6 mm or more separates it from the surrounding soil. This roof is sculptured with a regular curvature, and its surface is remarkably well-finished. In bigger nests, the thick roof extends down the sides of the deeper chambers, and thus a flattened sphere results. The intervening space, or "atrium", is then continuous around the outside of the shell, except that the latter abuts the soil in several places. During the excavation of several nests, we hoped to collect the sphere in one piece; this was never successful, although a few levels of chambers were taken out intact.

When the sphere was first exposed during the excavations, few ants if any were present in the atrium. Soon however some individuals emerged from small openings which occur around the upper region of the sphere; some are encircled by neatly moulded flanges, 2–3 mm thick and curling outward to form tyre-shaped rings (Fig. 2). These openings are approximately 5–20 mm in diameter. When the shell was sliced away, chambers (up to 80 mm across) filled with brood and adults were seen (Fig. 2, 3). Various insect prey were scattered among the larvae on chamber floors. The chambers were more or less horizontally aligned, and stacked in several levels separated by layers of soil 2–19 mm thick. The chambers led into one another by way

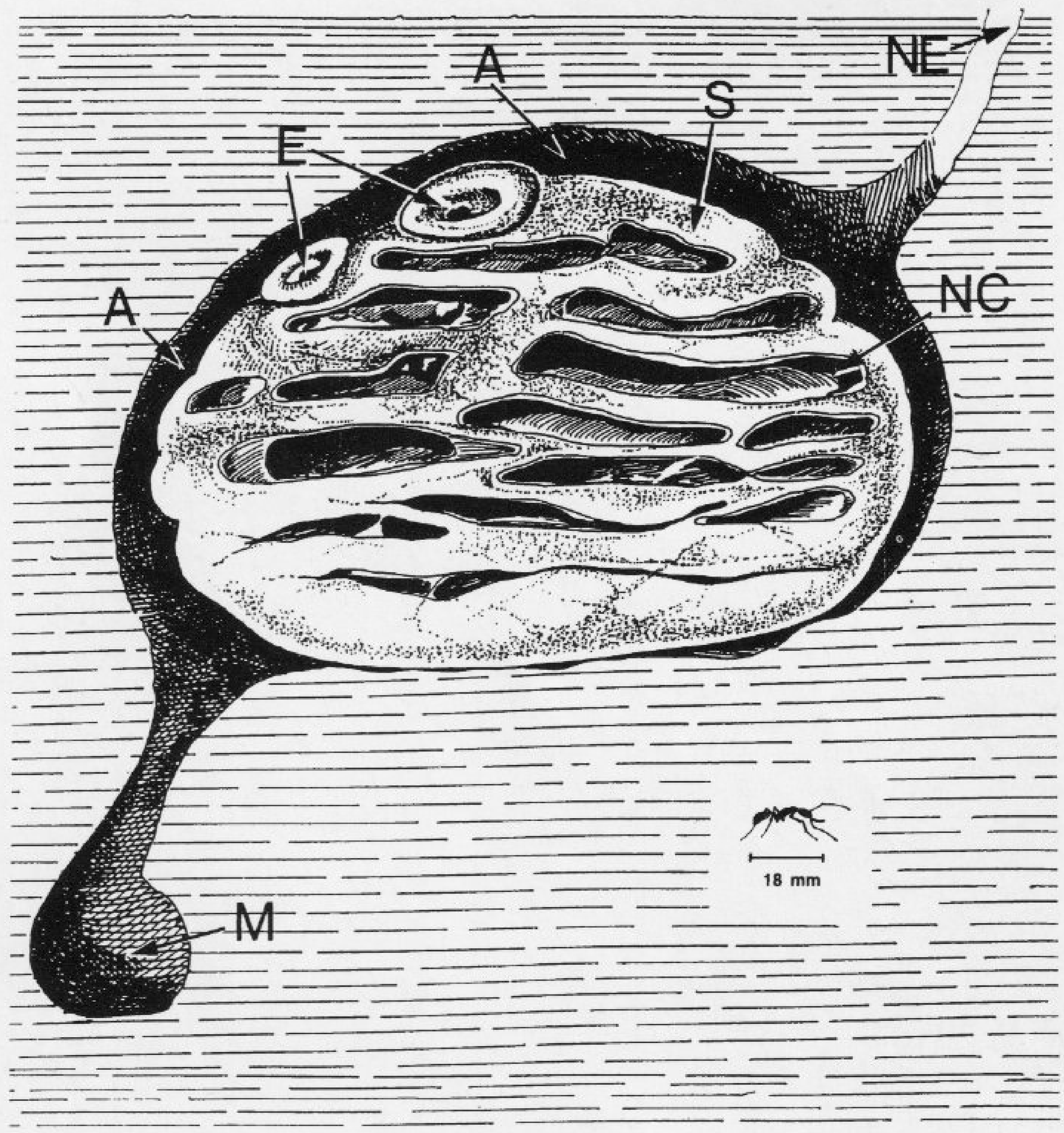

Figure 1. Large underground nest (hundreds of workers) of *H. saltator*. This drawing is reconstructed from photographs and field sketches (refer to text for measurements). For clarity, the height of chambers has been exaggerated, while the tunnels leading to the entrance and the refuse chamber have been shortened. A worker (18 mm long) has been included to give an approximation of scale.
A: atrium; NE: entrance tunnel; S: nest sphere, cut away to reveal the chambers (NC); E: openings into the sphere; M: kitchen midden

of large round holes in their floors or ceilings, and those on the same level could be subdivided by thin walls into several parts, or they could constitute one continuous space. The uppermost chamber often had a high ceiling (up to 20 mm) due to the vaulted roof. Additional chambers dug underneath are lower in height (8–11 mm). In many colonies having less than 100 workers, as was often the case in Jog Falls, we did not find flanged openings.

The inside of the chambers looked very smooth (already mentioned by Maschwitz 1981 a). A detailed investigation revealed that most surfaces are lined with a brown papery material, consisting mainly of strips of empty cocoons, with pieces of insect cuticle, wings, and vegetable material meshed in (Fig. 4). Such wall-papering was absent outside the sphere. Cocoon fragments appear to be glued together, because they do not fall apart when the lining is lifted off the wall with a pair of forceps.

The entrance gallery, approximately 8–10 mm wide, leads downward and opens into the atrium. Another tunnel extends from the lower reaches of the atrium to a small refuse chamber approximately 50 to 250 mm deeper in the soil (Fig. 1). It is filled with a moist, blackish-brown mass of prey remains (crickets, moths, spiders and

Figure 2. Parts of a nest of *H. saltator* near Jog Falls. (a) The atrium cavity has been cut away revealing (beneath a horizontal root) the nest sphere with its flanged openings. The refuse chamber is visible at the lower left corner (arrow). (b) Close up of the larger flanged opening, with a worker present just within. (c) Vertical cross section of the chambers inside the nest sphere

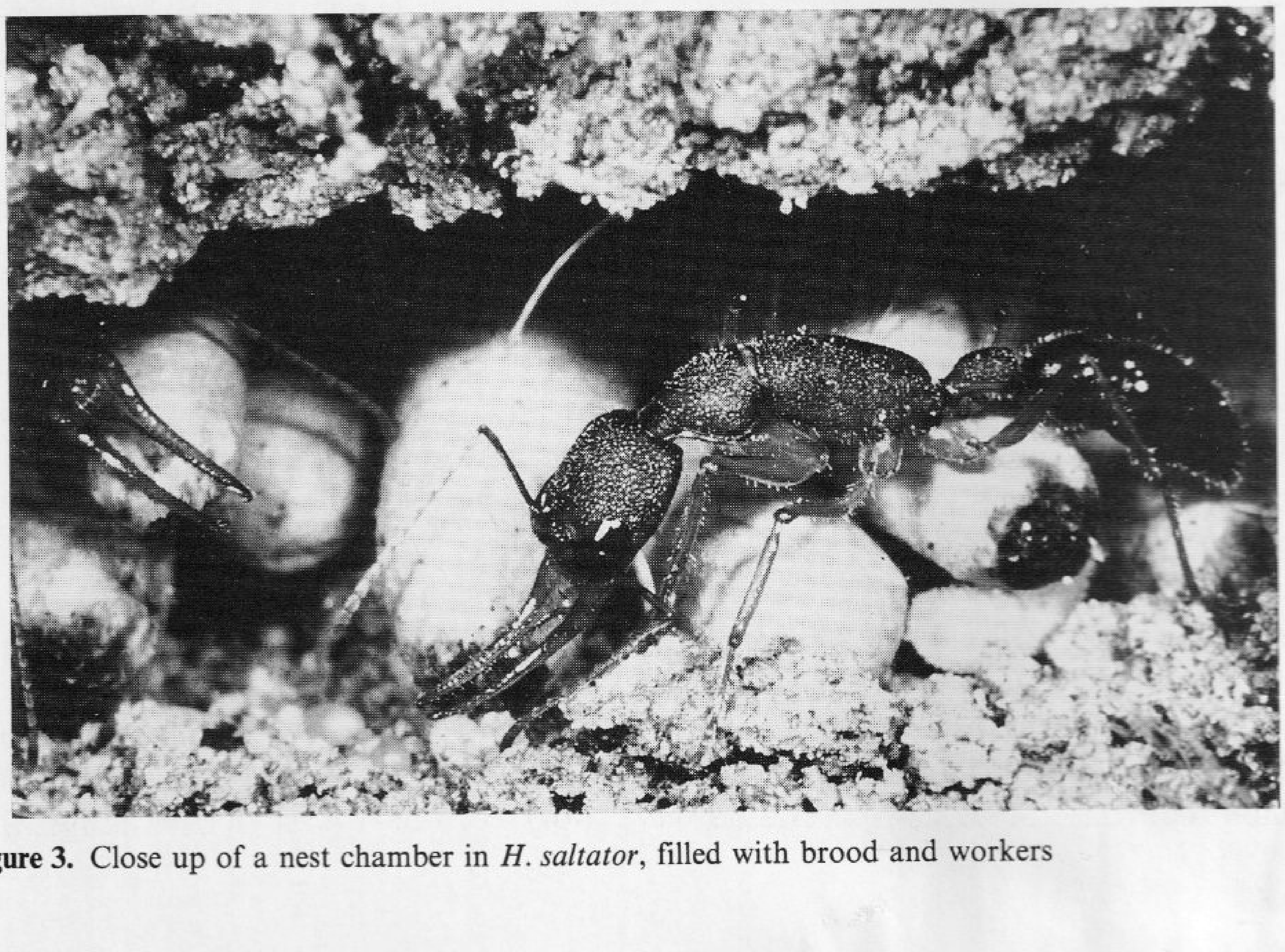

Figure 3. Close up of a nest chamber in *H. saltator*, filled with brood and workers

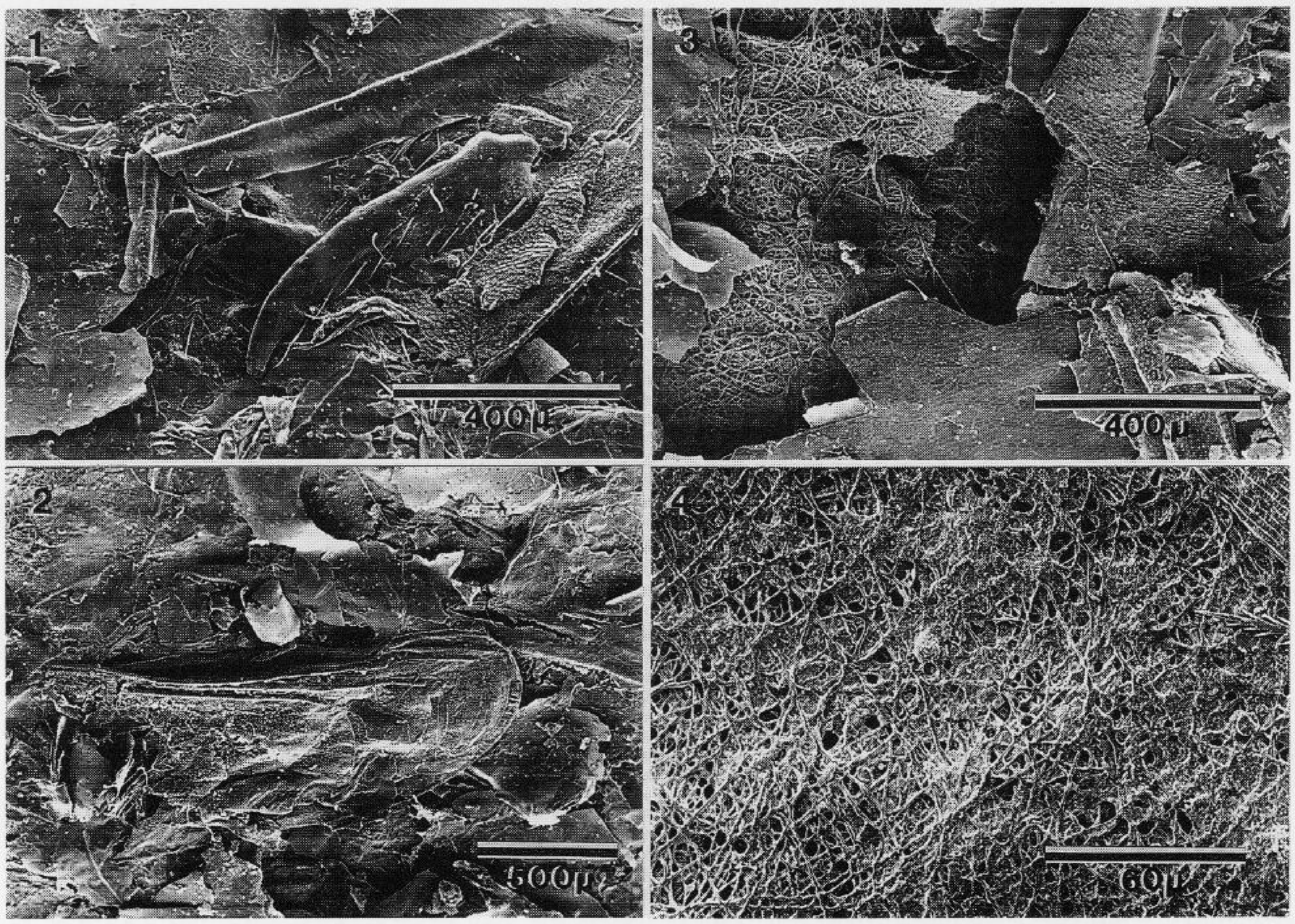

Figure 4. SEM-photographs of the "wall-paper" lining the nest chambers in *H. saltator*. Pieces of insect cuticle (1), wings (2), plant material (1) (3) and soil can be found intermeshed among the strips of cocoons (4)

other arthropods but no *Harpegnathos* workers), together with numerous isopods and live fly larvae. These larvae hatched in our laboratory, and belonged to family Milichiidae (H. P. Tschornig, pers. comm.).

In the Jog Falls area, *H. saltator* was primarily found inside and at the edge of evergreen forests, whereas in Bangalore the ants nested in a *Eucalyptus* plantation. A common feature of these two habitats was the thick layer of leaf litter on the ground, which seems to be where the ants prefer to forage. In some colonies the nest entrance was a simple hole hidden by leaf litter. In others the entrance was surrounded by a disk of small dried leaves or other plant debris, which had clearly been arranged there by the workers. In one of the Bangalore nests, the entrance hole was surrounded by a shallow disk (200 mm in diameter) of *Eucalyptus* fruits. These had been collected in the vicinity, because several returning workers were observed depositing them around the entrance.

Discussion

Ponerine ants nest either in soil or in rotting tree trunks lying on the surface. Most ground-nesting species build relatively simple nests consisting of an irregular system of chambers and tunnels. Some species have short-lived nesting sites, and emigration is frequent. When the nest is more permanent, chambers can extend very deep (e. g. Lévieux, 1965). Alternatively, in *Paltothyreus tarsatus*, very long foraging galleries are built just below the surface (Hölldobler, 1980; Braun et al., 1994). Despite this ability to move significant volumes of soil, ponerine ants generally build nests with a simple architecture. Often, they only seem capable of modifying and enlarging underground cavities (e. g. abandoned termite galleries). *Harpegnathos* nests are thus remarkable because soil is sculptured into complex shapes (similar to termite constructions), and the inhabited chambers are enclosed in a shell which is isolated from the surrounding earth.

What is the function of the atrium cavity and the flanged entrances to the nest sphere? To reach the inhabited chambers, a returning forager must, after descending the entrance gallery, cross the atrium and then climb through an opening in the shell. We speculate that the atrium helps prevent flooding of the nest chambers. In the Indian sub-continent, there is a long dry period before the monsoon rains; during the latter, large volumes of water are absorbed in the soil. Water-logged ground probably threatens shallow ant nests. However the design exhibited in *H. saltator* may afford protection against flooding, because the atrium and the compacted shell insulate the ant chambers from the soil environment. Thus seeping water is likely to run down the atrium and be diverted away from the inhabited chambers. The presence of a refuse chamber which is always deeper than the nest sphere provides another clue to the function of the atrium. This structure was always conspicuous because of the many wriggling fly larvae inside. In all the other ponerine ants which we have studied, prey remains are carried outside the nest. We cannot think of any adaptive benefits associated with the underground refuse dumps of *H. saltator*, and another line of thought may be followed: the deeper chamber has a different function, and its use as a midden is secondary. We suggest that it is built together with the atrium cavity, as part of a design which serves to drain water away from the nest sphere. How the adult flies locate their underground breeding grounds became clear after observing flies that were riding on the petiole of returning foragers; the flies hugged the ant's body and were not easily disturbed. Maschwitz (1981 b) made similar observations in Sri Lanka and identified the flies as belonging to family Milichiidae, while Musthak Ali et al. (1992) also reported seeing flies entering the nests in this way. The fly larvae, which we found in all the nests excavated, probably have a beneficial effect for the ants, because they eat the organic debris discarded by the ants, thereby keeping the refuse chambers from clogging up.

New colonies of *H. saltator* are founded by solitary queens. In Jog Falls, an incipient nest with less than 20 workers and eggs and larvae consisted simply of a shallow blind-ending tunnel. We do not yet clearly understand how the ants build and enlarge the nest sphere. The presence of an intervening space between the surrounding soil and the shell enables the ants to work on its outside, which explains its polished appearance and regular curvature. The uppermost chamber with its vaulted roof seems fundamental to the design of the sphere, and it probably remains unchanged as further chambers are excavated underneath. The atrium is gradually extended, and it reached under the lowermost chamber in some nests. The refuse chamber is probably relocated deeper in the ground, because it was always lower than the sphere. The architecture of two nests suggested that lateral expansion of the chambers sometimes happens, and then the shell seems recycled as an internal partition. Pebbles and roots were sometimes incorporated in the sphere. Note that walls are unlike the "carton" of other ants, which is built from particles of wood, dry vegetable material, and soil glued together with sugary secretions collected by the ants (Hölldobler and Wilson, 1990).

How is the quilt-like layer covering the inside of the nest sphere assembled? *Harpegnathos* workers possess a large sternal gland between the 6th and 7th abdominal segments (Jessen et al., 1979). No behavioral function has yet been found for this gland, but it is possible that its secretions are involved in "wall-papering" pieces of pupal cocoons and material collected outside (Fig. 4). Only one other ant is known where workers use cocoons to wall-paper their nest chambers. In the ponerine *Prionopelta amabilis*, the wooden galleries housing pupae are often lined with several layers of cocoons (Hölldobler and Wilson, 1986). The surfaces of these "wall-papered" galleries are considerably drier than those of other galleries. In the laboratory nests of *H. saltator* we observed that workers tore up newly eclosed cocoons into strips. These were used to cover pupating larvae and to plug up holes in the artificial nests. Sometimes pieces of cocoons were placed on the glass ceilings. The "wallpaper" lining of the chambers may have a significant function in stabilizing the humidity inside the nest sphere, thereby favouring successful larval development.

From an ultimate perspective, the elaborate nest structure of *H. saltator* can be assumed to be essential for colony survival, and thus it is adaptive for the ants to invest time and labour in nest construction. We do not know whether colony emigration ever occurs, but we think it is unlikely for several reasons: (i) as a consequence of their energetic cost, the nests should not be readily abandoned; (ii) in the event of emigration to a new site, the ants would initially inhabit a simple nest, where their survival may be imperiled; (iii) adaptations for efficient nest relocation are lacking. Nestmates are carried above ground instead of being recruited with chemical signals, and thus nest-moving is a slow process (our data; see also Maschwitz, 1981 a). Moreover, since eggs lie singly on the floors of the chambers (they do not adhere in packets as in many ponerine ants), they would have to be carried one by one (two at the most) in the event of an emigration. Maschwitz (1981 a) noted that colonies are very stationary. This is also supported by our discovery of four nests having more than 300 workers; the presence of several levels of large chambers indicated that such nests were probably relatively old.

Queens and males are produced annually in *H. saltator*, and mated dealate queens then start new colonies. Later in a colony's ontogeny, the queen is replaced by several gamergates (Peeters and Hölldobler, unpublished). In ponerine ants where gamergates reproduce exclusively, colonies multiply obligatorily by fission (Peeters, 1991). The process of colony fission remains poorly understood, but it is likely that opportunities are provided by the emigration of workers and brood. Consequently we speculate that colony fission never occurs in *H. saltator*, and older colonies are potentially immortal since new gamergates differentiate every year.

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