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The Giant Nests of the African Stink Ant *Paltothyreus tarsatus* (Formicidae, Ponerinae)[1]

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ABSTRACT

Fourteen nests of the ponerine ant *Paltothyreus tarsatus* were excavated in Kenya and in the Ivory Coast. All colonies contained only one mated queen. The worker population varied markedly between colonies, reaching 2444 adults in one case. Nests consisted of many chambers located 30 cm to more than 150 cm below the surface. The construction and arrangement of the chambers were not particularly elaborate, but the associated horizontal tunnel system (5–15 cm below the surface) was most remarkable. In one nest, over 130 m of shallow subterranean tunnels were uncovered. An area of 1200 m² was covered by the tunnel system of another nest. Through multiple tunnel exits the ants are able to reach almost any spot in their foraging area. In some nests we found a second horizontal tunnel system, 50–80 cm below the surface, which connected nest chambers several meters apart.

Key words: *ants; foraging; monogyny; nests;* Paltothyreus; *Ponerinae; polydomy; queen; reproduction.*

PALTOTHYREUS TARSATUS, a member of the ant subfamily Ponerinae, is widely distributed throughout Africa south of the Sahara (Wheeler 1922). It is a hunter and a scavenger. Although the workers forage individually, they can recruit nestmates with chemical signals when retrieving large or more abundant prey items (Hölldobler 1984). The nests of *P. tarsatus* are built in the soil. As noted in previous field studies, they have multiple entrances, and mature colonies occupy rather large surface areas (Lévieux 1965; Kalule-Sabiiti & Banage 1977; Hölldobler 1980, 1984; Déjean *et al.* 1993). In the course of continuing ecological investigations of *Paltothyreus* we have found that their nests can be substantially bigger in area and more populous than previously thought.

MATERIALS AND METHODS

We excavated a total of 14 nests. Four colonies were collected in the Shimba Hills Reserve (Kwale district, south of Mombasa, Kenya); three during July–August 1978 and one during May 1991. The latter in particular was very thoroughly dug out by two persons over 4 days (>40 man-hours) and unexplored tunnels still remained. We began at an active entrance, and followed the shallow foraging galleries by gentle digging with a trowel. A considerable amount of clearing was often required in order to proceed; branches and roots were cut and ground litter was removed. Once large concentrations of workers were found, vertical digging proceeded. The excavated tunnels were left uncovered, and overnight digging activity by the ants led to the detection of many side tunnels. The lengths of the tunnels were measured between intersections. The number and location of exit holes were not recorded in this colony. Another ten colonies were collected in the National Park of the Comoé in the Ivory Coast during August 1992 and February–May 1993.

RESULTS

Paltothyreus tarsatus colonies nest primarily in forested areas, but also in the transition zone between forest and savanna. Our most detailed data on nest structure were obtained from two colonies in Kenya. In one colony (August 1978), we especially examined the tunnel system in the "core area" where most of the brood and the queen were collected (Figs. 1 and 2). There were about 25 exit holes leading either to tunnels 5–15 cm below the surface, or directly to the inhabited chambers. The latter were also connected together by subterranean galleries (Fig. 2). The core area could be recognized by the crater-shaped nest entrances and the conspicuous mounds of soil and refuse piles (containing prey and cocoon remains); this was not the case in all colonies. The majority of the nest chambers were located 30–150 cm below the surface. The larger

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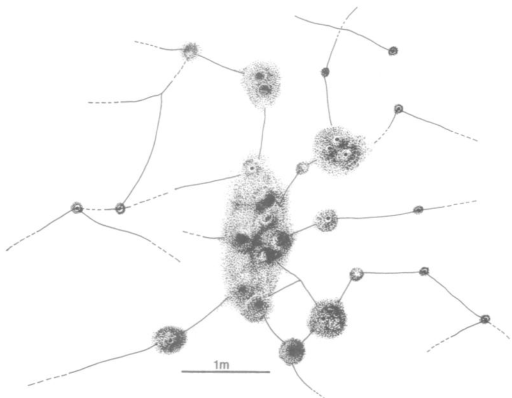

FIGURE 1. Core area of a *P. tarsatus* nest (Kenya; August 1978), showing the funnel-shaped entrances surrounded by mounds of soil and refuse piles. The underground tunnels leading to the foraging grounds are also indicated, together with exit holes.

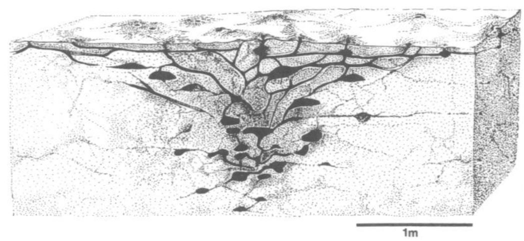

FIGURE 2. Vertical section through the central chambers and connecting galleries of a *P. tarsatus* nest (Kenya; August 1978). This drawing is based on numerous field sketches and photographs taken during the excavation.

chambers, measuring approximately 25 × 5 × 5 cm, were found closer to the surface (*ca* 30–100 cm depth), the smaller chambers (4 × 3 × 1 cm) were mostly located at a depth of 100–150 cm. In this particular nest we identified more than 40 inhabited chambers. We collected from those chambers, from adjacent galleries and on the surface, a total of 1 dealate queen, 916 workers, 82 larvae, 45 pupae, 4 males, and 1 alate queen. We confirmed by dissection that the dealate queen was inseminated. Despite our intensive efforts we probably did not uncover all nest chambers, missing especially more alate queens and males. As previously noted (Hölldobler 1980, 1984) an extensive system of shallow tunnels led from the nest chambers to the surrounding foraging grounds (Fig. 1).

In a second colony from Shimba Hills (May 1991), we aimed to reveal the entire network of shallow tunnels (Fig. 3). The excavation started in an open, grassy area, but the galleries soon led to two different forested areas. Over 130 m of foraging galleries were uncovered. This excavation revealed that one colony can be distributed into several nesting sites, labelled A, E, and F (Fig. 3). In A, where chambers reached deeper than elsewhere, we collected 518 workers, 20 larvae, 6 eggs, and 1 dealate queen (also inseminated); there were 208 workers and 2 larvae in E, and 77 workers in F. In addition we caught 102 workers walking along the uncovered foraging galleries. Thus a total of 905 workers were collected throughout the range of this colony. However we were unable to follow all the foraging galleries, or to excavate deep chambers completely. This may explain why so few brood were collected, especially cocoons (although one cocoon was carried by a worker along a foraging gallery, indicating that they were present at this time of the year).

Two additional nests excavated in July 1978 also yielded only one inseminated queen for each colony; the numbers of workers were 392 and 446, respectively. In both cases, however, we were not yet familiar with the complexity of the architecture of *Paltothyreus* nests, and it is therefore possible that we did not uncover other major parts of the nests.

Our excavations of ten *P. tarsatus* nests in the Ivory Coast (1992 and 1993) revealed a similar organization as found in Kenya. The size of the nest populations varied greatly (Table 1), suggesting that some colonies were younger, while others may have been collected incompletely. One colony excavated

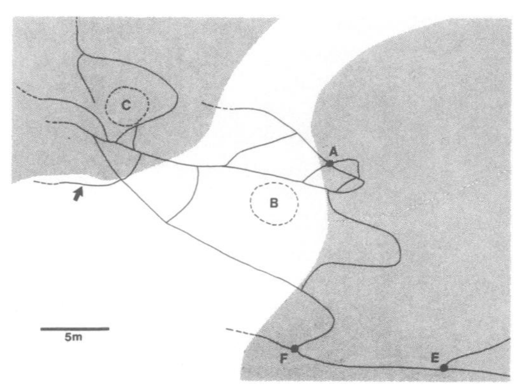

FIGURE 3. The subterranean tunnel system of a *P. tarsatus* nest (Kenya; May 1991). Only shallow tunnels are indicated (5–10 cm below the surface). The arrow indicates the spot where the excavation began. A, F, and E are the locations of deep chambers where workers and brood were collected. Many workers were also found above ground around B and C. Stippled areas indicate forest and thicket vegetation; clear area represents grassland.

TABLE 1. *Demographic data from 10 nests of* Paltothyreus tarsatus *excavated in the Ivory Coast.*

Nest	Dealate queen	Alate queens	Males	Workers	Cocoons	Larvae	Eggs
Aug. 1992	1	0	0	385	499	458	218
Aug. 1992	1	0	0	157	120	7	35
Aug. 1992	1	59	0	247	68	91	19
Aug. 1992	1	73	5	688	764	241	0
Aug. 1992	1	36	0	377	30	164	0
Feb. 1993	1	0	0	1552	94	1376	208
Feb. 1993	1	466	696	1191	444	129	945
Feb. 1993	1	408	131	1522	166	2016	139
April 1993	0	0	0	2444	1118	2789	177
May 1993	0	0	0	692	580	915	163

in April 1993 was considerably larger (numbers of adult workers, cocoons and larvae). In all colonies, however, we found only one dealate queen. In four nests we found a second system of deeper horizontal tunnels, 50–80 cm below the surface, which led to another network of chambers, 3 to 5 m from the currently occupied core area. Whether these chambers were entirely abandoned or had just been evacuated could not be determined. In one nest we measured the subterranean foraging tunnels covering an area of up to 1200 m^2.

DISCUSSION

Ants of the subfamily Ponerinae usually build relatively simple nests in the soil or in rotting wood. A few species exhibit more complex nest architecture, *e.g., Harpegnathos saltator* (Peeters *et al.* 1994). Although the design and construction of the chambers of *P. tarsatus* nests are not particularly elaborate, the huge scale of their system of chambers and tunnels is remarkable. Our data indicate that colonies can be considerably larger than previously assumed. In the Ivory Coast Lévieux (1967) excavated 5 colonies and found an average number of 350 workers per colony, with a maximum of 450 workers. In Cameroun, Déjean *et al.* (1993) collected two colonies with 260 and 311 workers. The larger worker populations in our study may be related to the completeness of our excavations. Colonies of *P. tarsatus* are large relative to other ponerine ants with a single queen (see Peeters 1993), although colonies of *Leptogenys distinguenda* can yield more than 30,000 workers (Maschwitz *et al.* 1989).

Our study also revealed that large *P. tarsatus* colonies can occupy more than one nesting site, several meters distant from each other, but connected by subterranean tunnels. This represents a special case of polydomy. Based on these new findings, we have to consider the possibility that some of the nests (10 to 20 m apart) which Hölldobler (1984) identified as belonging to separate colonies, may in fact be parts of one and the same colony. Generally, colony size may be underestimated since, given the availability of numerous underground connections between different parts of the colony, brood and workers can be evacuated as the ants detect the vibrations caused by human digging. Hölldobler (1984) observed that tandem running is used to recruit nestmates when parts of a nest are accidentally destroyed (as opposed to trail laying during foraging); this specialization suggests that relocation within an existing nest complex may occur frequently.

The home range of *P. tarsatus* foragers above ground is generally not greater than 5 m and is usually considerably smaller (Hölldobler 1984). However, the underground trunk routes with multiple exit holes enable the foragers to travel securely to many points in the colony's territory (up to 40 m away from the main nest), before commencing to forage above ground. Mark and recapture tests indicate that individual ants show substantial fidelity in the use of specific exits (Hölldobler 1984). Such decentralized territories allow harvesting benefits from throughout the interior of the large territory while reducing predation on foragers (Hölldobler & Lumsden 1980, Hölldobler & Wilson 1990). It also enables precise orientation in the restrictive lighting conditions of forests (Hölldobler 1980).

We found only one dealate queen in all colonies excavated. This confirms the finding of Lévieux (1965) that *P. tarsatus* colonies are monogynous. They are established by semi-claustral foundation (C. Peeters, pers. obs. in South Africa; Villet *et al.* 1989). Given the highly dispersed character of the nest complexes, it is interesting to speculate about the mechanism of queen control in this species. In the laboratory we isolated a large group of over 500 workers without their queen. No eggs were laid until after 11 weeks; after 15 weeks more than 10 eggs were found. These observations suggest that the workers were previously inhibited by the queen. Since the colonies are large, we assume that reproductive inhibition is pheromonal, and that the queen signal is distributed to workers throughout the nest. How this is achieved is currently being investigated in our laboratory.

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