

Soil-binding pilosity and camouflage in ants of the tribes Basicerotini and Stegomyrmecini (Hymenoptera, Formicidae)

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Summary. Workers of the tropical ant tribes Basicerotini and Stegomyrmecini possess two dominant forms of setae on the dorsal surfaces of the body and outer surfaces of the legs: longer “brush” hairs with splintered distal ends, and shorter “holding” hairs that vary among species from plumose to blade-shaped or filiform. The two usually but not invariably occur together to create a double layer. The brush hairs evidently scrape or otherwise capture fine particles of soil, while the holding hairs help to keep them in place next to the surface exoskeleton. As the worker ages, the soil accumulates as a thin, mud-like layer, greatly enhancing the overall camouflage of the body. The material appears to be primarily or entirely exogenous; no special secretory cells were found (in *Basiceros manni*, studied for this purpose) that might contribute cryptically colored chemicals or adhesive substances to hold the soil in place.

A. Introduction

Since the time of Fabricius and other pioneering taxonomists, the shape and distribution of setae have been used prominently in the classification of ants. This is particularly true of certain cryptobiotic species, such as those belonging to the tribes Basicerotini, Dacetini, and Stegomyrmecini, the setae of which are often spatulate, knob-shaped, plumose, squamiform or otherwise bizarre in shape. With rare exceptions no function has been established for the setae; they have simply been described as part of taxonomic diagnoses.

We report here a first detailed analysis of the anatomy and function of the distinctive pilosity that characterizes the basicerotine and stegomyrmecine ants.

The Basicerotini have a strongly disjunct distribution, ranging throughout the New World tropics and in the Old World, from tropical Asia to Melanesia and Queensland. Their 7 genera (*Basiceros* Schulz, 1906; *Creightonidris* Brown, 1949; *Eurhopalothrix* Brown and Kempf, 1960; *Octostruma* Forel, 1912; *Protalaridris* Brown, 1980; *Rhopalothrix* Mayr, 1870; *Talaridris* Weber, 1941) comprise approximately 40 described species characterized by thick, hard integuments; depressed head shapes; bent, flattened antennal scapes with the subbasal angle often forming a prominent anterior lobe; frequently arcuate-linear or otherwise peculiarly shaped mandibles; greatly reduced segmentation of maxillary and labial palps; and prominent and

heavily sclerotized labra that project forward through the mandibular gap (Brown and Kempf 1960; Brown 1974). Members of the genera *Eurhopalothrix* (= *Rhopalothrix* part.) and *Basiceros* have been shown to be predators of small arthropods in rotting wood and litter of the forest floor; *E. heliscata* of Singapore and Malaysia appears to specialize to some extent on termites (Wilson 1957; Wilson and Brown 1984; Wilson and Hölldobler 1986).

The Stegomyrmecini are among the smallest and rarest of all ant tribes, being known from only two species (*Stegomyrmex connectens*, *S. manni*) from Central and South America respectively. They resemble Basicerotini and in particular *Basiceros*, the most primitive living member of the Basicerotini, but differ in their possession of broad frontal lobes, as well as in their deep, broad antennal scrobes, placement of the compound eyes below instead of above the scrobes, and the plan and manner of closing of the mandibles (Brown and Kempf 1960). To date nothing has been learned of the biology of these ants except that, like *Basiceros* and other Basicerotini, their anatomy renders them extremely difficult to find in their natural habitat.

B. Materials and methods

The study was conducted with live and freshly preserved material of *Basiceros manni* collected at La Selva, Costa Rica, together with collections of other basicerotines and stegomyrmecines in the Museum of Comparative Zoology, Harvard University. The surface structure of the ants was investigated with the aid of an AMR 1000 A scanning electron microscope.

For histological investigations live specimens were fixed in Carnoy, embedded in methylmethacrylate, and sectioned 5–8 μ thick with a Jung Tetrander microtome (Rathmayer 1962). The staining was Azan (Heidenhain).

C. Results

I. Basiceros manni Brown and Kempf, 1960

The pilosity pattern most thoroughly analyzed to date is that of *Basiceros manni*, illustrated in Figs. 1–4. Over large parts of the body, including most of the dorsal surface of the head, alitrunk, and first gastric tergite, as well as on the outer surfaces of the femora and antennal scapes, the pilosity consists primarily of two types of setae. We call

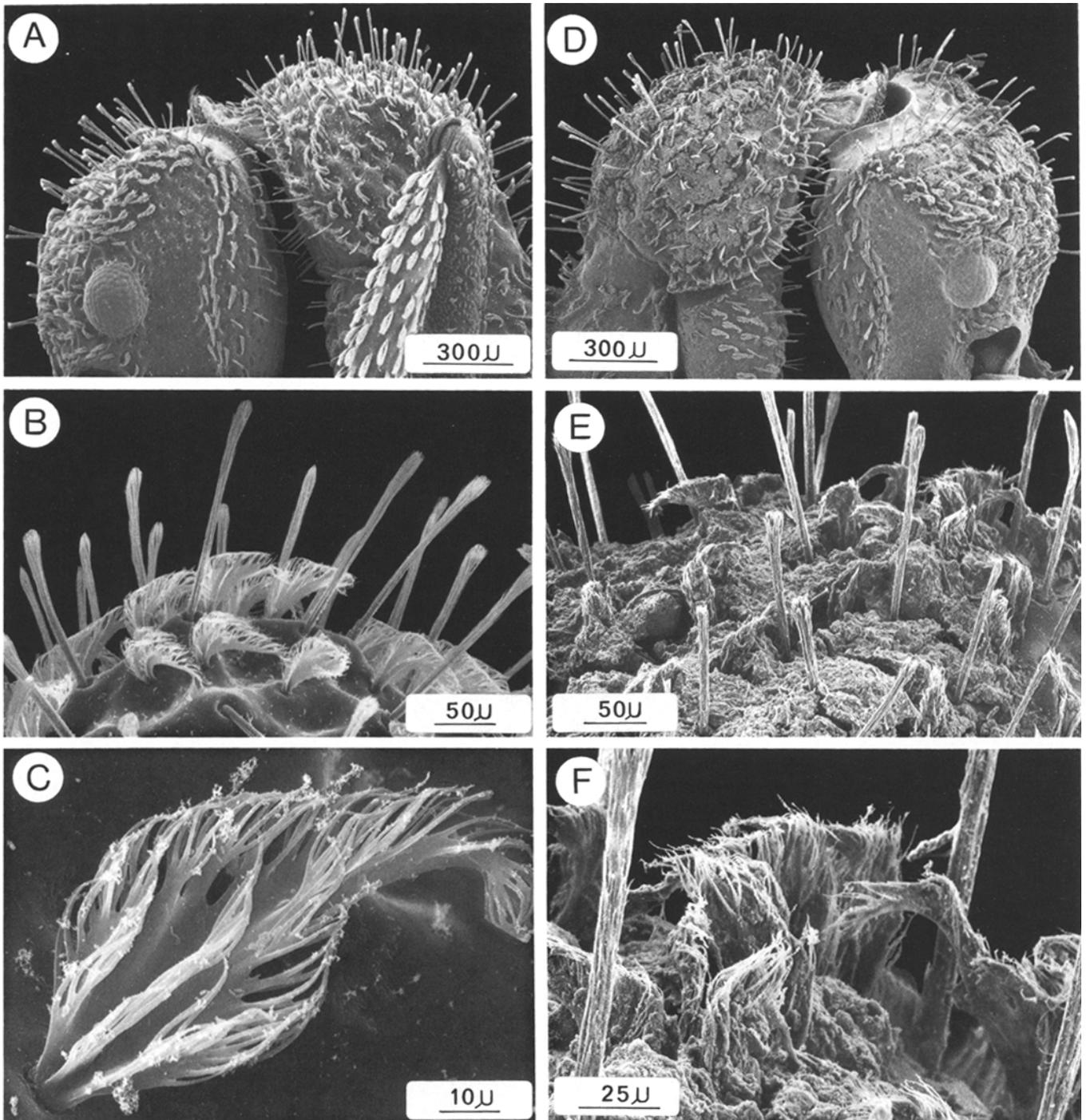


Fig. 1 A–F. SEM views of the dorsal surface of the bodies of *Basiceros manni* workers. On the left is shown a young worker, which has not yet accumulated a film of soil, in 3 frames as follows: **A** portions of the head and thorax; **B** close-up of the prothorax, showing the two layers of soil-collecting hairs; **C** a plumose hair from the lower layer. On the right is an older worker, which has acquired a well-developed film of soil on its dorsal body surface: **D–F** views comparable to those of **A**, **B**, and **C**

the first kind “brush” hairs. They are relatively long, stand erect off the cuticle, and are splintered at the distal end, creating a rough resemblance to a broom. The second kind, the “holding” hairs, are plumose and typically bent or curled with the result that part of their shaft runs parallel to the cuticular surface. The brush and holding hairs usually occur together, forming a double layer over the dorsal sur-

faces of the occiput, the scapes, the pro- and mesonota, petiole, and postpetiole, and gaster. An intermediate form of seta is found on the outer surfaces of the femora and tibiae (Fig. 4).

The brush hairs appear to aid in the collection of fine particles of soil, while the holding hairs capture and fix the particles in place. Young workers, which care for the

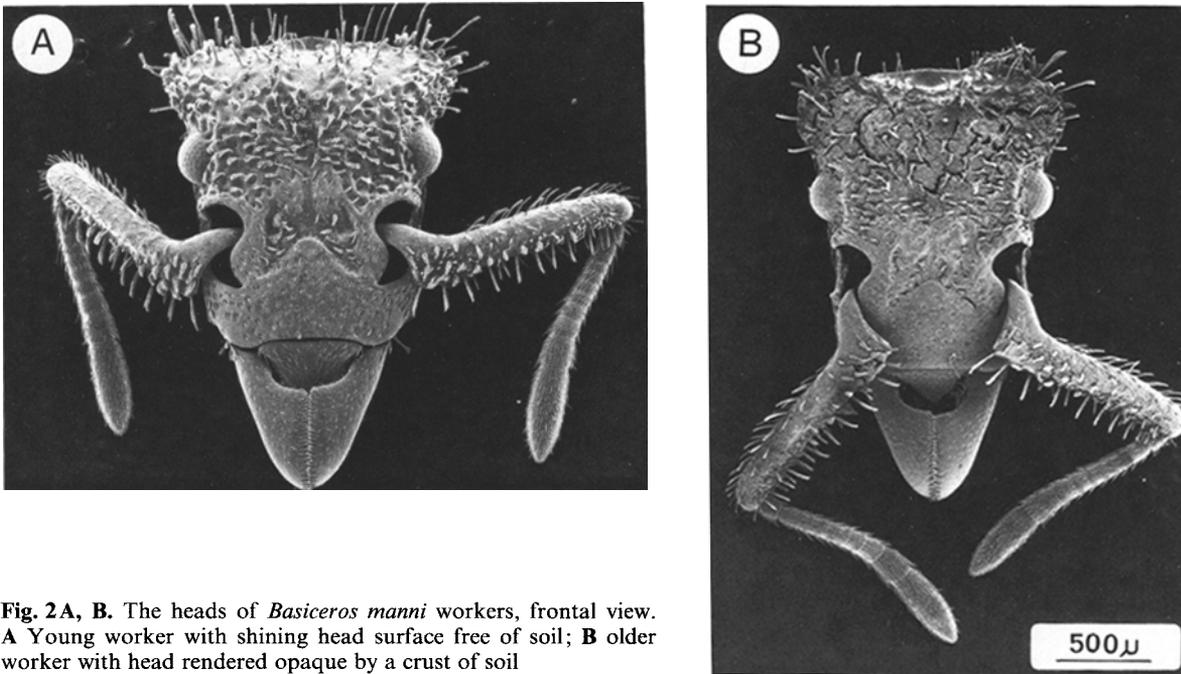


Fig. 2A, B. The heads of *Basiceros manni* workers, frontal view. **A** Young worker with shining head surface free of soil; **B** older worker with head rendered opaque by a crust of soil

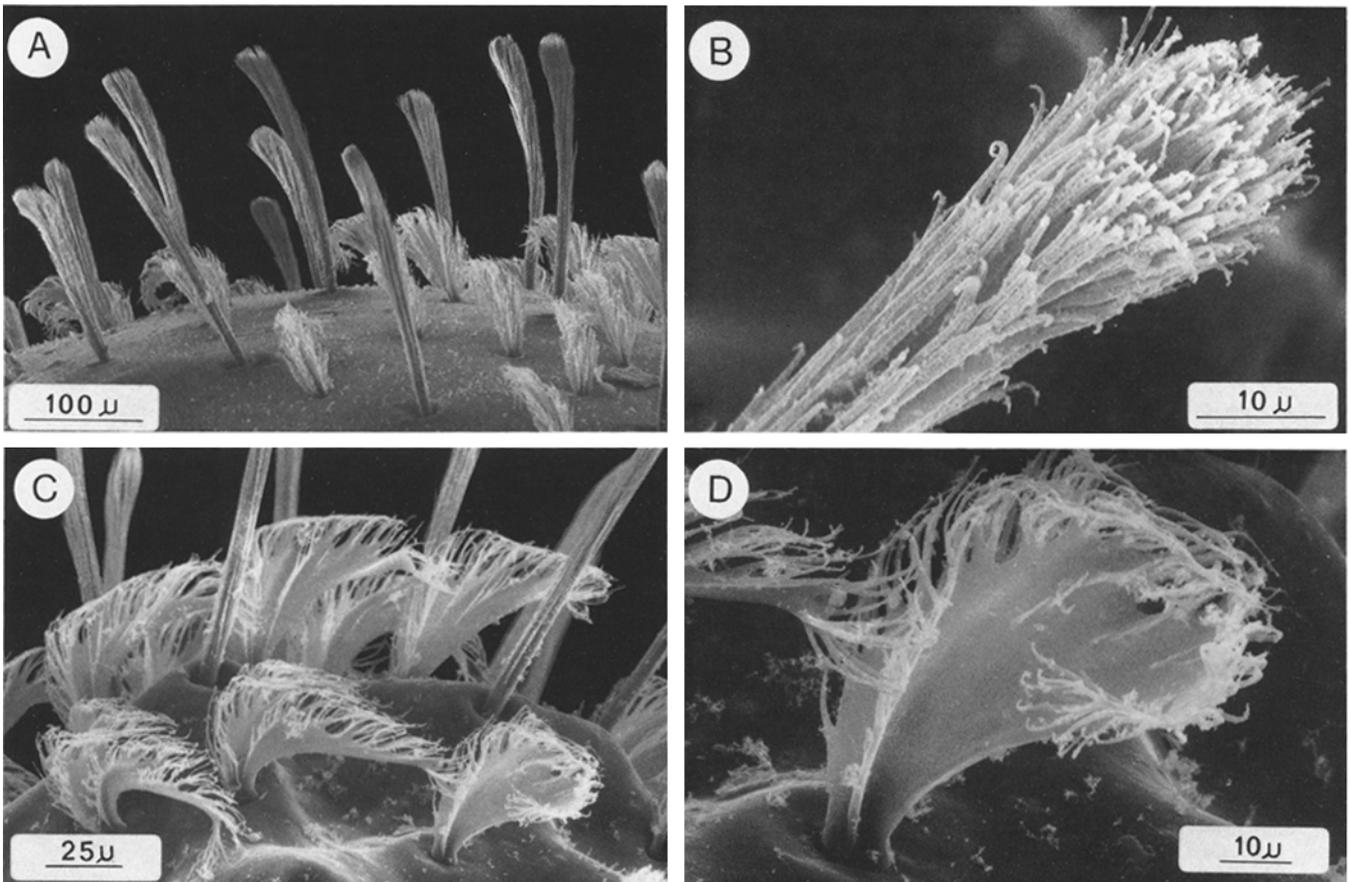


Fig. 3A–D. Views of the setae of a *B. manni* worker. **A** The two layers of setae on the first gastric tergite; **B** distal end of a brush seta on the thorax, belonging to the upper layers; **C** plumose setae on thorax, belonging to the lower layer; **D** close-up view of a plumose seta on thorax

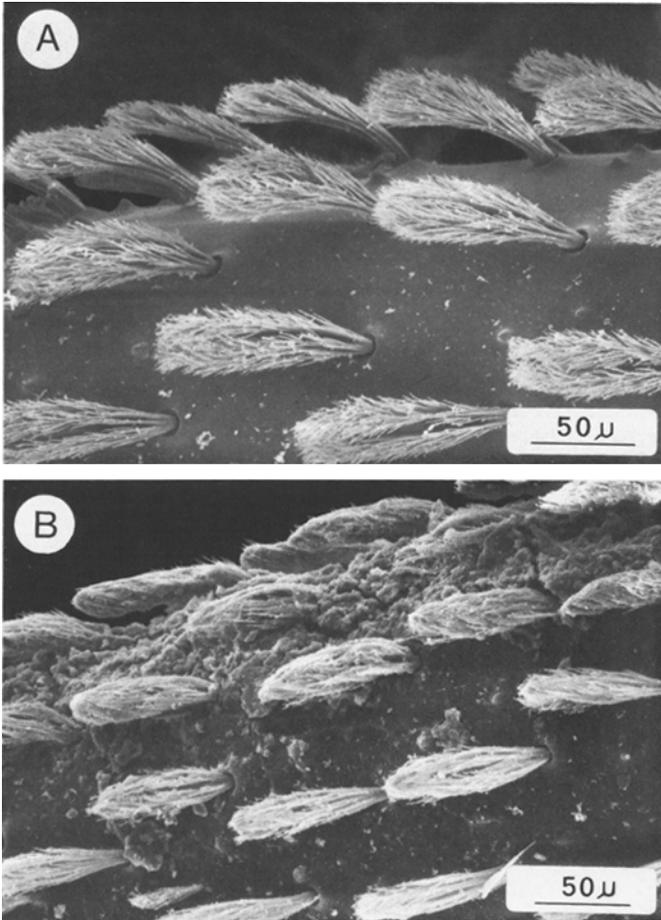


Fig. 4A, B. Plumose setae on the femora of *B. manni* workers. **A** Outer femur surface of a young worker, still free of soil; **B** outer femur surface of an older worker, with soil particles caught in and between the setae

brood and attend other duties inside the nest, are free of soil. As a consequence their body surfaces are dully shining. Older workers, which concentrate on hunting outside the nest as well as nest construction and repair, gradually accumulate soil particles until the material forms a continuous, mud-like sheet over parts of the body bearing the specialized setae (see Figs. 1, 2, 4). This material renders the covered surfaces opaque and colored identically to much of the soil and litter surface over which the older workers forage.

To the human eye, and presumably that of many visually orienting predators, the ants are difficult to see while walking along in their natural habitat, and virtually invisible when standing still. The effect is enhanced by the fact that *Basiceros manni* workers are among the most slowly moving ants we have encountered in our joint lifetime experience, which extends to over 200 of the approximately 270 ant genera found worldwide. When observed in an undisturbed state, the entire worker force often stands perfectly still for minutes at a time, even holding their antennae in place. And when workers in motion are disturbed by being uncovered or touched with a pair of forceps, they freeze into immobility for up to several minutes (Wilson and Hölldobler 1986).

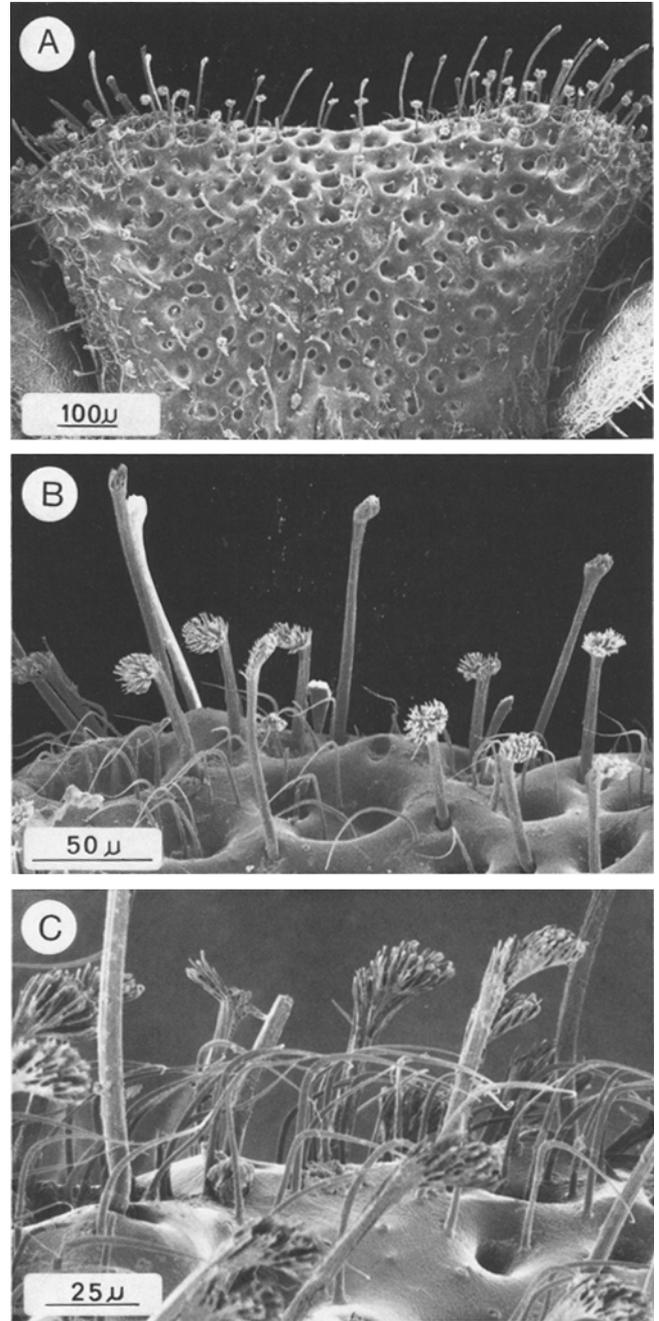


Fig. 5A–C. Views of the head of a worker of *Stegomyrmex connexens*. **A** Frontal view of rear half of head, showing the two layers of setae, the upper brush hairs and lower, wire-shaped holding hairs; **B, C** two close-up views of the two layers of setae

The camouflaging material is mostly or entirely exogenous. Under SEM examination it appears identical to fine soil particles in the original nest material. When we transferred living colonies to plaster-of-Paris nests, the workers began to accumulate white particles from the substrate on their body surfaces. Finally, a detailed investigation of longitudinal histological preparations of *B. manni* workers failed to reveal secretory cells associated with the setae that might contribute to the camouflage layer by the addition of either cryptically colored chemicals or adhesive sub-

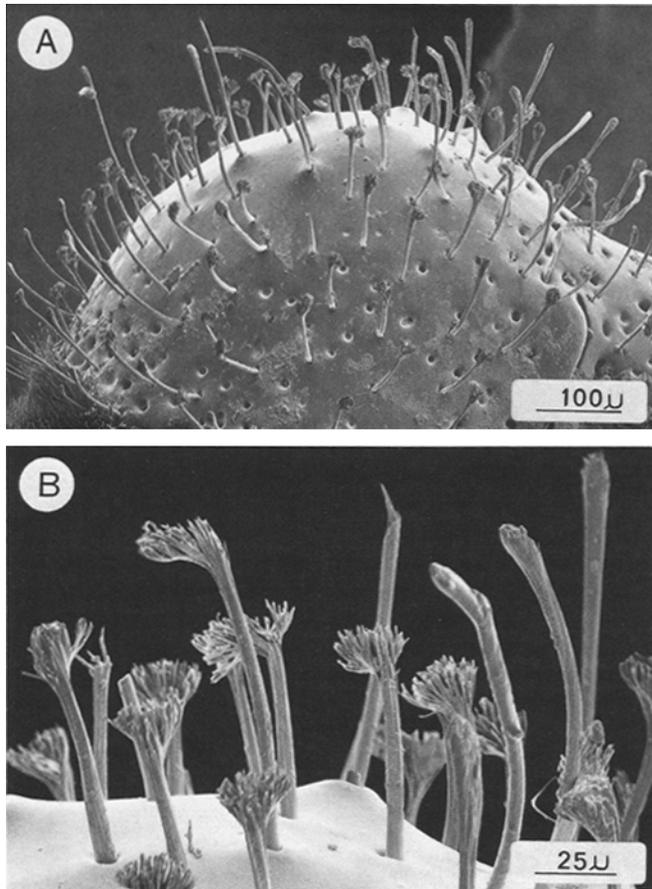


Fig. 6 A, B. Prothorax of a *Stegomyrmex connectens* worker showing the two layers of soil-collecting setae in distant (A) and close-up (B) views

stances that hold the soil. Instead, the histological investigations confirmed that the soil particles, which individually measure not more than $10\ \mu$, are densely packed onto and between the plumose setae.

Basiceros manni workers have a very well-developed metapleural gland, with approximately 200 glandular cells on each side. It is possible that this relatively large size of the gland is associated with the need for higher production of antibiotic substances (Maschwitz et al. 1970) to prevent microorganisms from growing more luxuriantly in the soil layer on the body.

II. *Stegomyrmex connectens* Emery, 1912

As illustrated in Figs. 5–7, the two-layered pilosity of this species is close enough in form to that of *Basiceros* to support the hypothesis, based on other features of anatomy, that the two genera are phylogenetically related. Three differences are worth noting: (1) the brush hairs are splintered closer to the tips, giving the hairs the look of a bottle brush; (2) the holding hairs are filiform rather than plumose; and (3) only brush hairs occur on the gaster. We have examined a worker from Barro Colorado Island, Panama (Sally Levings; Museum of Comparative Zoology collection) that

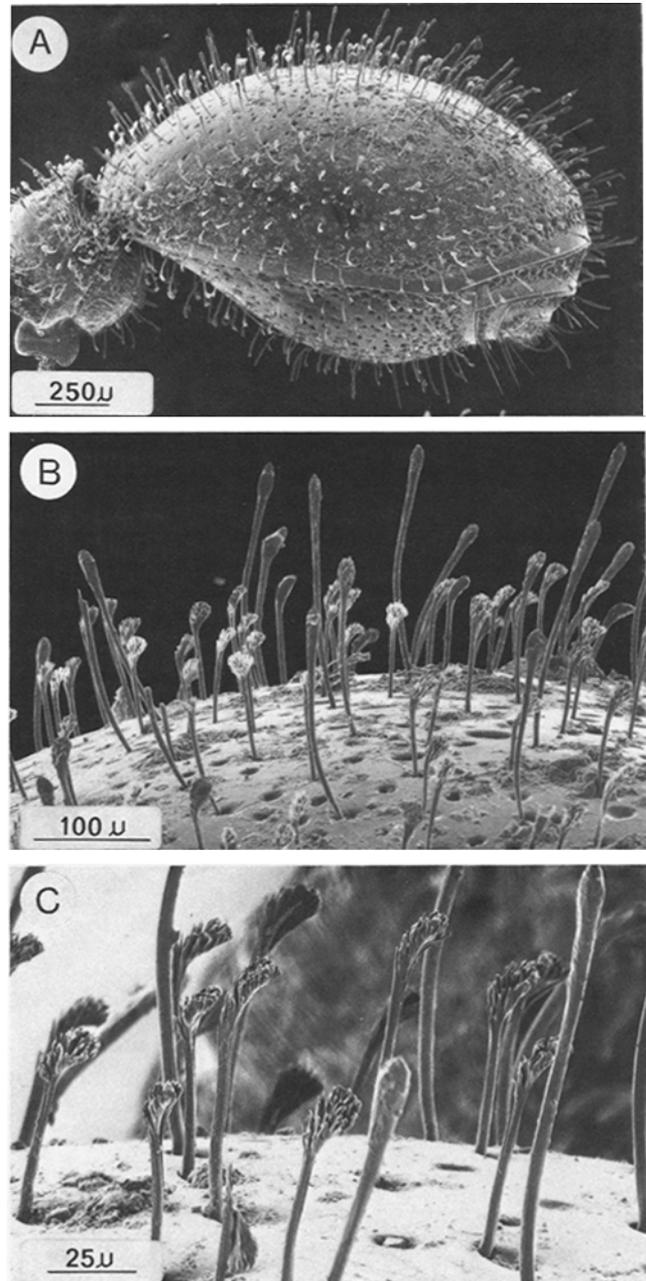


Fig. 7 A–C. Postpetiole and gaster of a *Stegomyrmex* in distant (A) and close-up (B, C) views. This part of the body bears only brush setae

bears a soil layer closely similar to that found in *Basiceros* workers.

III. *Protalaridris armata* Brown, 1980

This remarkable basicerotine species, only recently described by Brown (1980) from the Pacific slope of the Andes in Ecuador and Colombia, is notable for the preponderance of holding hairs (Figs. 8, 9). These structures range over the body and appendages in approximately the same positions as the plumose holding hairs of *Basiceros* and are

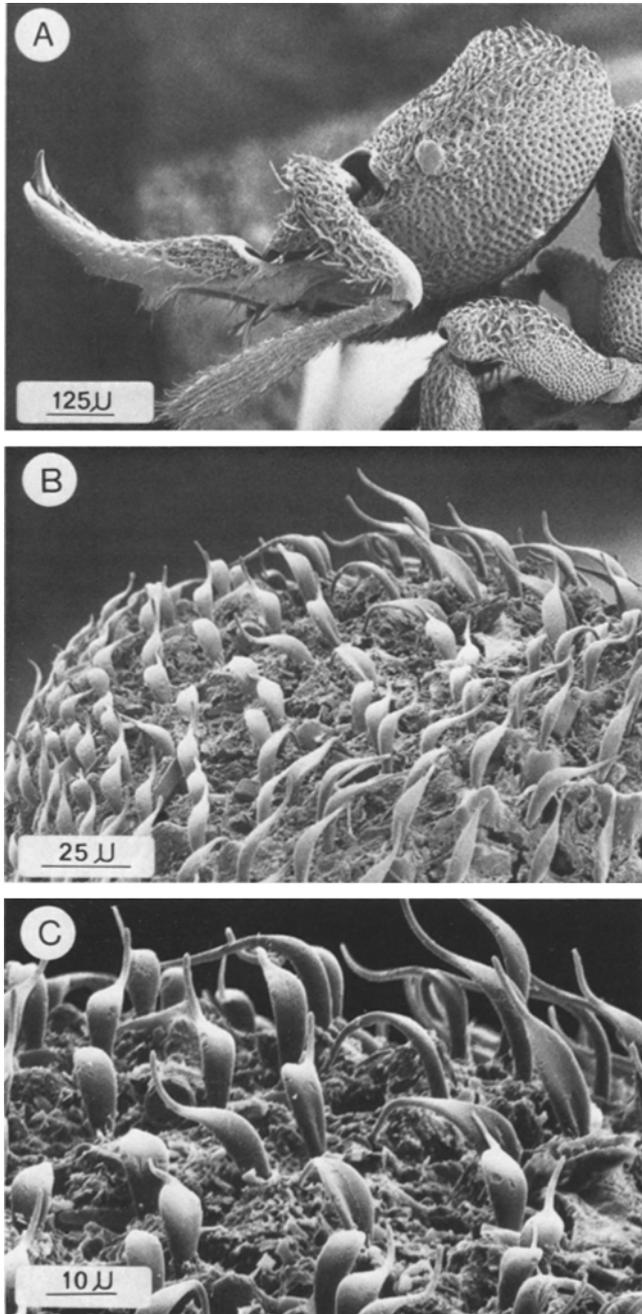


Fig. 8 A–C. Head of a worker of the basicerotine ant *Protalaridris armata*. **A** Side view of the entire head; **B**, **C** different portions of the occipital region, showing the blade-shaped holding setae

especially dense on the occiput. They are blade-shaped and clearly associated in some worker specimens with a soil covering (see Fig. 9C). Brush hairs, which closely resemble those of *Basiceros manni*, are sparse and limited to the first 2 gastric tergites.

IV. *Octostruma batesi* Emery, 1894

The small, exclusively Neotropical members of *Octostruma* are typified by *O. batesi*. As in *Protalaridris*, holding setae greatly outnumber brush setae, with the latter being limited

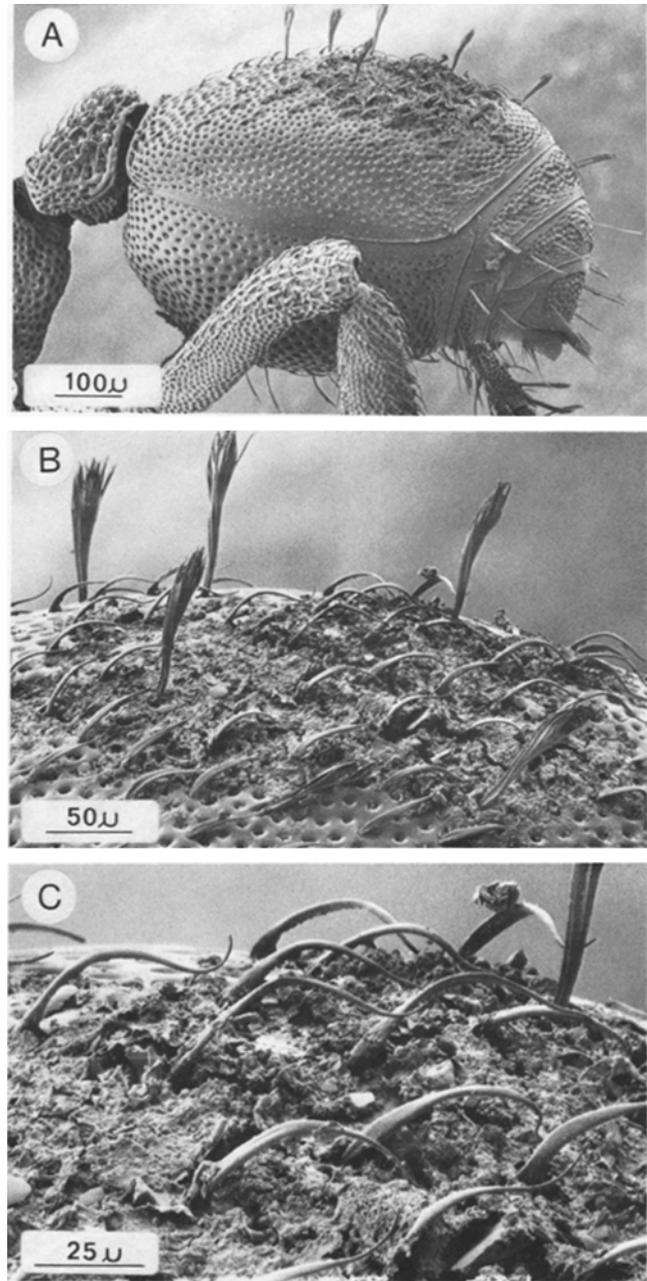


Fig. 9 A–C. Postpetiole and gaster of *Protalaridris armata*. **A** Distant view of the two body parts, showing the restriction of the soil-collecting setae to the upper body surface and legs; **B**, **C** close-up views of the brush setae and lower, blade-shaped holding setae

to the gastric tergites. The holding setae are distinctive in shape, being thick, hairlike, and curved strongly so that the tips closely approach or touch the cuticular surface. On the head they are largely absent from the occiput but massed on the vertex and frons, where they are associated with a soil layer (see Fig. 10A).

V. *Eurhopalothrix* spp.

The two species chosen, *E. bolawi* (Mayr, 1870) of Central and northern South America (Fig. 11) and *E. biroi* (Szabó,

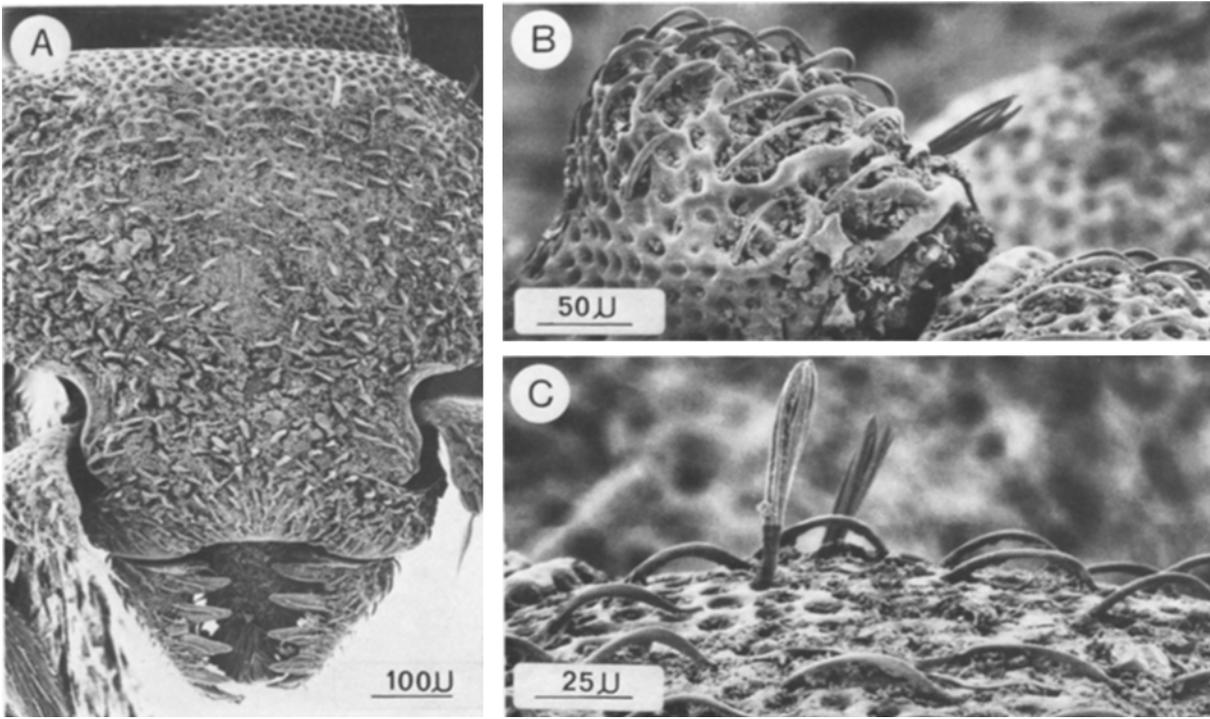


Fig. 10A–C. Views of a worker of the basicerotine ant *Octostruma batesi*. **A** Frontal view of head, with holding hairs and soil layer visible; **B** dorsal surface of petiole, showing holding hairs and soil; **C** dorsal surface of first gastric tergite, showing upper layer of brush hairs and lower layer of recumbent holding hairs

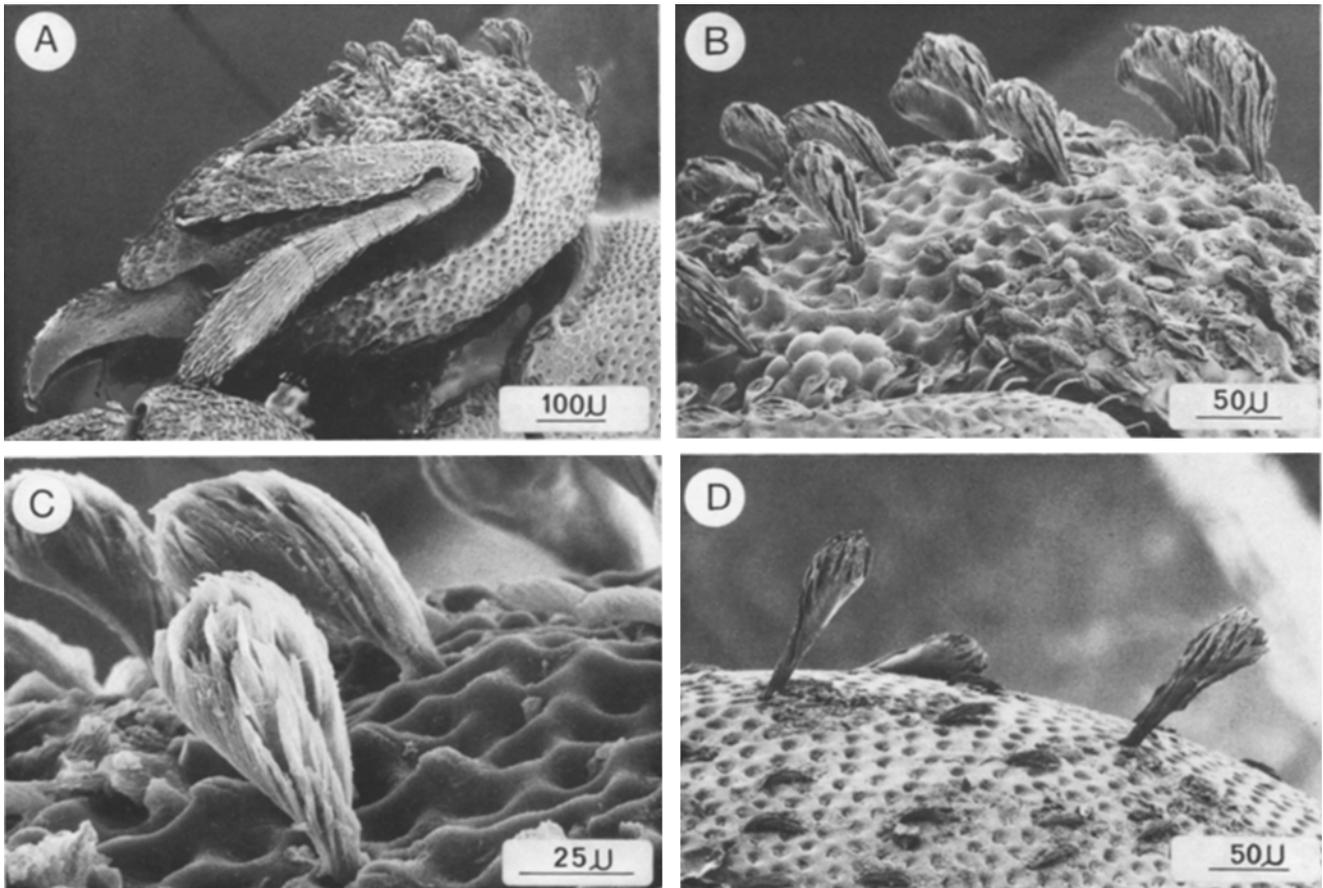


Fig. 11A–D. Views of a worker of the basicerotine ant *Eurhopalothrix bolai*. **A** Side view of head with conspicuous brush setae on the dorsal surface; **B**, **C** close-up of brush setae and much smaller holding setae on dorsal surface of the head; **D** brush and holding setae on dorsum of first gastric tergite

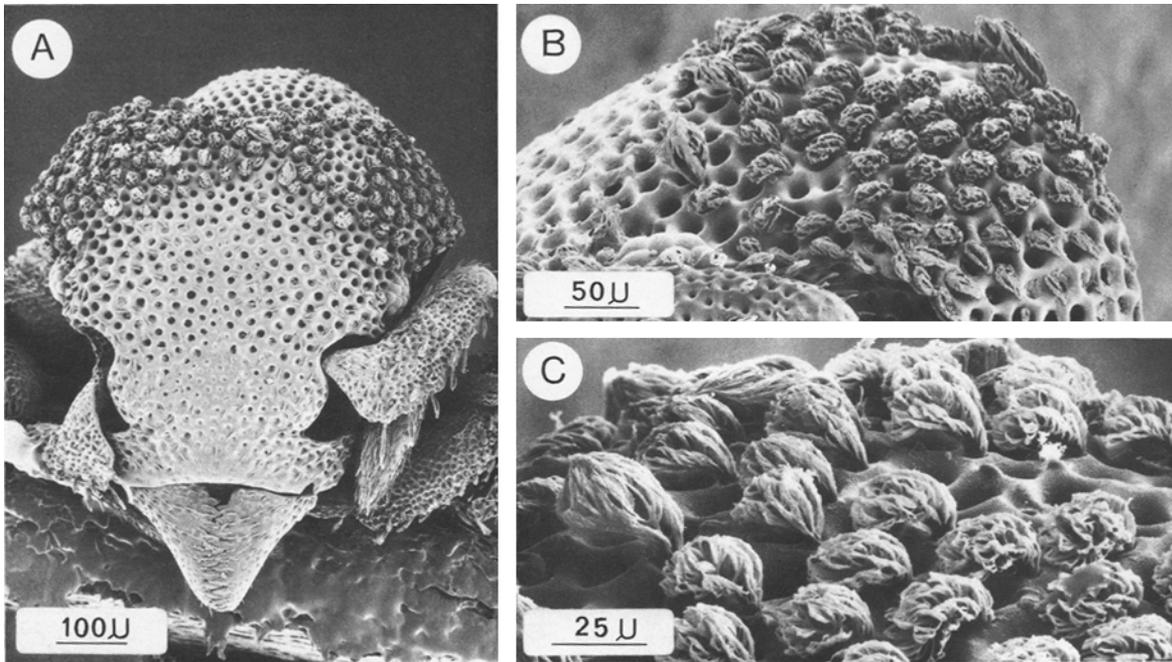


Fig. 12A–C. Views of the basicerotine ant *Eurhopalothrix biroi*. A Front view of head, with brush setae massed on the occiput; B, C close-up views of the brush setae on the occiput

1910) of New Guinea (Fig. 12), illustrate the striking variation in pilosity that occurs within the genus. They share the basic form of the brush setae, which are splintered most or all the way to their bases. But they differ markedly in the pattern of distribution of the setae. Also, *E. biroi* possesses only short brush setae, and these are limited to a crown-like arrangement on the head. (A third species, *E. heliscata* of Singapore and Malaysia, has a nearly one-layered distribution of modified setae over the entire dorsal surface of the body and appendages; see Wilson and Brown 1984.)

C. Discussion

Our study of the basicerotines and *Stegomyrmex*, including behavioral observations on *Basiceros manni*, has revealed at least one key role of the bizarre pilosity that has long been known to characterize these ants. It seems clear the most distinctive shapes of what we call the brush and holding hairs are well suited to capture and bind a soil layer, which in turn contributes to the camouflage of the ants. But this cannot be the whole story. A mystery remains concerning the variation in the shapes of the hairs from species to species, which we have detailed at high magnification for the first time. For example, why are the holding hairs plumose in *Basiceros* but filiform in *Stegomyrmex*? The answer, if one exists in terms of Darwinian adaptation, may lie in mechanical principles not yet understood. The evolution of the seta form may have been further constrained by peculiarities in the size, foraging patterns, and detritus particles of each of the species in turn.

Striking variation also occurs in the location and density of the pilosity, and this also demands an explanation. In general, the hairs – as well as the soil films associated with them – are located in dorsal positions where they are most

needed for camouflage. In other words, the surfaces of the ants most affected are also those most likely to be seen by birds, lizards, and other predators searching from above or the side of the ants. But there the consistency ends. Compare, for example, the dense cluster of hairs on the occiput of *Eurhopalothrix biroi* (Fig. 12A) with the virtual absence of hairs on the occiput of *Octostruma batesi* (Fig. 10A). Furthermore, as the outline drawings and taxonomic descriptions of Brown and Kempf (1960) illustrate so well, the hairs of basicerotine species are often greatly reduced in number or absent. For example *Eurhopalothrix brevicornis*, *Rhopalothrix diadema*, and *Talaridris mandibularis* each have a triple row of sparse hairs across the occiput; *Rhopalothrix plaumanni* has the cephalic hairs limited to its clypeus, frons, and antennal lobes; and *R. stannardi* lacks specialized cephalic hairs altogether. Detailed studies of the behavior and ecology of these and other cryptobiotic ants, with special reference to the functions of the pilosity, will almost certainly prove a very rewarding exercise in evolutionary biology.

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