

RECORDED
IN ANTING

Insectes Sociaux, Paris
1986, Volume 33, n° 1, pp. 70- 84

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ECOLOGY AND BEHAVIOR OF THE NEOTROPICAL
CRYPTOBIOTIC ANT *BASICEROS MANNI*
(HYMENOPTERA : FORMICIDAE : BASICEROTINI)

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Reçu le 8 juillet 1985

Accepté le 25 novembre 1985

SUMMARY

We report here the first detailed observations of a member of the Neotropical genus *Basicros* (*B. manni*), which possesses the largest and anatomically most primitive workers and queens within the ant tribe Basicerotini.

1. Colonies of *Basicros manni* were found nesting in small rotting logs and a leguminous seed pod on the floor of Costa Rican rain forest. The mature colony composition is a single dealate queen and approximately 50 workers. New queens and males eclosed during late March, in the dry season.

2. *B. manni* workers and queens are cryptically colored to an extreme degree, a condition enhanced by the accumulation of soil and litter particles on the body surface with the aid of a double layer of plumose hairs (fig. 1-3). They are also among the slowest-moving of all ants and "freeze" into immobility for minutes at a time when disturbed.

3. The workers capture a wide diversity of insects, including beetle larvae and (in the laboratory) centipedes, termites, and *Drosophila* adults. The prey are fed directly to the larvae. So far as known the workers forage singly and do not recruit.

4. Emigration is facilitated by a communication behavior apparently preliminary to adult transport: workers that have encountered suitable nest sites tug at the appendages of nestmates, causing them to search on their own. Workers also carry nestmates to the new sites, but less commonly.

5. The repertory size is unusually small for myrmicine ants. A relatively simple temporal division of labor occurs, with young workers functioning more as nurses and older ones as foragers (fig. 4, tables I, II). The ovaries are maximally developed in the youngest workers, evidently in association with the laying of trophic eggs. Conversely, the poison gland reservoir reaches its greatest size in older workers, in association with increased predatory activity.

6. Overall, *B. manni* has a behavioral repertory comparable in complexity but not in detail to that of *Eurhopalothrix heliscata*, the only other basicerotine species studied to date.

This study has revealed at least four notable features in the behavior of *Erebomyrma nevermanni* not directly related to caste, namely defensive queen retinues, the use of trunk trails during foraging, the collection of arthropod eggs, and the absence of adult transport during colony emigration.

ACKNOWLEDGMENTS. — I am grateful to Bert HÖLDOBLER for advice given during the present study, and to Robert M. FAGEN for calculating the maximum number of behavioral categories from my data. The research was supported in part by a grant from the National Science Foundation BSR-84-21062.

References

- BROWN W.L., 1973. — A comparison of the Hylean and Congo-West African forest ant faunas. In: B.J. MEGGERS, E.S. AYENSU, and W.D. DUCKWORTH, eds., *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, pp. 161-185. Smithsonian Institution Press, Washington, D.C.
- CARPENTER F.M., 1930. — The fossil ants of North America. *Bull. Mus. Comp. Zool. Harv.*, 70, 1-66, 11 pl.
- EIDMANN H., 1936. — Oekologisch-faunistische Studien an sudbrasilianischen Ameisen. *Arbeit. Phys. Angew. Entomol. Berlin-Dahlem*, 3, 26-48, 81-113.
- ETTERSHANK G., 1966. — A generic revision of the world Myrmicinae related to *Solenopsis* and *Pheidologeton* (Hymenoptera: Formicidae). *Australian J. Zool.*, 14, 73-171.
- FAGEN R.M., GOLDMAN R., 1977. — Behavioural catalogue analysis methods *Anim. Behav.*, 25, 261-274.
- OSTER G.F., WILSON E.O., 1978. — *Caste and Ecology in the Social Insects*. Princeton Univ. Press, Princeton, N.J.
- WHEELER W.M., 1914. — The ants of the Baltic amber. *Schrift. Physical.-ökon. Ges. Königsberg* 55, 1-142.
- WILSON E.O., 1962. — The Trinidad cave ant *Erebomyrma* (= *Spelaemyrmex*) *urichi* (Wheeler), with a comment on cavernicolous ants in general. *Psyche* (Cambridge), 69, 63-72.
- WILSON E.O., 1976. — Behavioral discretization and the number of castes in an ant species. *Behav. Ecol. Sociobiol.*, 1, 141-154.
- WILSON E.O., 1984. — The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.*, 16, 89-98.
- WILSON E.O., 1985a. — Invasion and extinction in the West Indian ant fauna: Evidence from the Dominican amber. *Science*, 229, 265-267.
- WILSON E.O., 1985b. — Ants from the Cretaceous and Eocene amber of North America *Psyche* (Cambridge), 92, 205-216.
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ZUSAMMENFASSUNG

**Oekologie und Verhalten der neotropischen, kryptobiotischen
Ameise *Basiceros manni* (Hymenoptera : Formicidae : Basicerotini)**

Wir berichten hier erstmals eingehende Beobachtungen an einer Art der neotropischen Gattung *Basiceros* (*B. manni*), die innerhalb des Tribus Basicerotini die grössten und anatomisch primitivsten Arbeiterinnen und Königinnen besitzt.

1. *B. manni* Kolonien wurden in verfaulenden Holzstücken und in Samenschoten von Leguminosen am Regenwaldboden in Costa Rica gefunden. Die ausgewachsene Kolonie besteht aus einer entflügelten Königin und etwa 50 Arbeiterinnen. Junge Königinnen und Männchen schlüpften Ende März, in der Trockenzeit.

2. Die starke kryptische Färbung der *B. manni* Arbeiterinnen und Königinnen wird durch die Anhäufung von Erde- und Streuteilchen an der Körperoberfläche noch verstärkt (Abb. 1-3). Die Ameisen bewegen sich sehr langsam und erstarren bewegungslos wenn sie gestört werden.

3. Die Arbeiterinnen fangen eine Vielfalt von Insekten, einschliesslich Käferlarven, und (im Laboratorium) Hundertfüsser, Termiten und *Drosophila* Fliegen. Die Beutetiere werden direkt an die Larven verfüttert. Soweit wir feststellen konnten foragieren die Arbeiterinnen einzeln. Futterrekrutierung scheint nicht vorzukommen.

4. Nestmigration wird durch ein Verständigungsverhalten ausgelöst, das dem Verhalten gleicht, das zu sozialem Trageverhalten führt: Arbeiterinnen, die geeignete Nestplätze entdeckt haben, zerren Nestgenossinnen an den Extremitäten, was diese veranlasst selbst den neuen Nestplatz zu suchen. Arbeiterinnen werden bisweilen auch von Nestgenossinnen getragen.

5. Für eine Myrmicine ist das Verhaltensrepertoire von *B. manni* ungewöhnlich klein. Eine vergleichsweise einfache, zeitliche Arbeitsteilung ist typisch für *B. manni*, wobei junge Arbeiterinnen vorwiegend als Brutpflegerinnen und ältere Arbeiterinnen als Futtersucherinnen fungieren (Abb. 4, tab. I, II). Junge Arbeiterinnen haben gut entwickelte Ovarien; offensichtlich legen sie trophische Eier. Umgekehrt ist die Giftdrüse bei älteren Arbeiterinnen besser entwickelt, vermutlich im Zusammenhang mit der grösseren Jagdaktivität.

6. Im allgemeinen gleichen das Verhaltensrepertoire von *B. manni* denen von *Eurhopalothrix heliscata*, die einzige andere Art des Tribus Basicerotini, die bisher untersucht wurde.

INTRODUCTION

The genus *Basiceros* comprises six known species limited to the tropical moist forests of South and Central America (BROWN and KEMPF, 1960; BROWN, 1974). It belongs to the myrmicine tribe Basicerotini, which has a strongly disjunct distribution, ranging throughout the New World tropics and in the Old World from tropical Asia to Melanesia and Queensland. The workers are the largest in the tribe, and in certain important characters they are more primitive than those of other genera, combining 12-segmented antennae; triangular mandibles with straight, opposable, multidenticulate masticatory borders; and a distinct metanotal groove. In some other res-

pects, however, *Basiceros* are as advanced as other members of the tribe, possessing deep antennal scrobes, peculiar wedge-shaped or disciform heads with posteriorly positioned compound eyes, bizarre pilosity, and (sometimes) serially arranged subpetiolar spines. They are altogether among the strangest-looking of all ants.

Despite their relative scarcity and cryptobiotic habits, some knowledge of the natural history of basicerotine ants has begun to accumulate. Studies of *Eurhopalothrix biroi* (WILSON, 1957) and *E. heliscata* (WILSON and BROWN, 1984) have revealed the workers to be predators on soft-bodied arthropods, with *heliscata* appearing to take termites preferentially. Their anatomy and behavior suit them very well to ferreting out and seizing prey in the tight spaces of the soil and litter where they live. The behavioral repertory and social organization of *E. heliscata* are rather simple, at least relative to most other myrmicine tribes examined to date. The workers have an elementary temporal division of labor, chemical recruitment, and chemotactic recognition of nest area, while trophallaxis and adult transport are rare or absent.

Because of their large size and relatively primitive anatomy (as well as the still unknown phylogenetic position of the Basicerotini), the species of *Basiceros* are especially deserving of study. Yet almost nothing has hitherto been learned about them, beyond several nest site and two prey records (WEBER, 1950; BROWN and KEMPF, 1960; BROWN, 1974). In fact the genus has proved difficult to find and is represented in museums by only a handful of nest series and solitary workers. Recently we succeeded in locating three queenright colonies in primary rain forest near Puerto Viejo, Costa Rica, and were able to study them under laboratory conditions for a month thereafter.

METHODS

The colonies were housed at first in simple laboratory nests consisting of shallow dishes 20×10 cm by 7 cm deep. Later they were placed in test tubes with 2.5 cm inner diameter in the bottom of which water had been trapped by a tight cotton wad, leaving a chamber 8 cm long for the ants to occupy. The ants were then allowed access to a 20×10 cm foraging chamber. The colonies were studied with the aid of a dissecting microscope at 10-12X magnification. The surface structure of the ants was investigated with the aid of an AMR 1000A scanning electron microscope.

The total number of behavioral categories (tables I, II) was estimated by the method of FAGEN and GOLDMAN (1977), in which the frequency distribution of the categories is fitted to a lognormal Poisson distribution.

RESULTS

Nest sites and colony populations

Three queenright colonies were located in primary rain forest along the 350-550 m segment of the Holdridge Trail of the La Selva Biological Station operated by the Organization for Tropical Studies. The station is located in Heredia Province, Costa

Rica, near the confluence of the Rio Puerto Viejo and Rio Sarapiquí (84°02'W, 10°26'N). The collections were made during March 22-27, 1985. The first colony was located in a large rotting pod of *Pentaclethra macroloba* (Mimosaceae) partially buried in leaf litter. When the two halves of the pod were pulled apart 8 workers, the queen, a worker pupa, and several larvae in different stages of development were found within a 5-cm-wide space. Another worker was found alone in the litter 20 cm from the pod. A careful search of the ground and litter through a 1-m radius of the nest failed to reveal other *Basiceros*.

The second nest was in a soft rotting log about 40 cm long and 20 cm wide, resting in litter on the forest floor. The ants were in two groups. One was in a 4-cm-wide chamber immediately adjacent to a pair of chambers containing fungus gardens of an attine ant (*Apterostigma* sp.); it consisted of 19 workers, 2 males, 18 worker pupae, 3 male pupae, one queen pupa, 24 larvae of various sizes, and two eggs. The other, in a similar-sized chamber 30 cm from the first, contained the queen and 25 workers. When this colony was transferred to an observation chamber for closer study, the workers evicted the *Apterostigma* workers mixed in with them, by dragging them away and dropping them, and cleared a circular area about 2 cm across in which the brood were placed.

The third colony was in a soft rotting log about 30 cm long and 25 cm wide. All of the ants were in a single group in two adjacent cavities which had a joint diameter of approximately 10 cm. The population was as follows: 1 dealate queen, 2 alate queens (one callow), 44 workers, 3 worker pupae, 5 queen pupae, 11 larvae, and 2 eggs.

A single dealate queen was discovered in a large rotting log in another La Selva locality on March 23, unaccompanied by workers or brood. Finally two workers were found in a third locality in secondary forest, about 2 m apart and evidently foraging. One was in a 15-cm-wide soft rotting log, the other in the rotting stem of a fallen palm frond.

Cryptic coloration and behavior

The camouflage of the *B. manni* workers and queen is the most effective we have personally encountered in the ants, and we have seen a large majority of the genera in living condition during field trips around the world. When the ants are standing still on their nest material, they are virtually invisible to the human eye and presumably also well concealed from most visually orienting predators, such as birds and lizards (see *fig. 1*). Experience showed that the colonies could best be located most readily by searching for the distinctive white larvae and pupae, then scanning for the adults around them.

The cryptic coloration of the *B. manni* exoskeleton is enhanced in the queen and older workers by the accumulation of fine soil particles in a dry, mud-like layer on the upper body surface (*fig. 2*). The material is evidently wiped off the surrounding soil and litter by the upper layer of hairs, which are shaped roughly like tapered bottle brushes. It is held in place by a lower layer of strongly curved "feather" hairs (*fig. 3*). A more detailed description of this unusual pilosity, along with similar patterns in other basicerotine and stegomyrmecine species, is given elsewhere (HÖLLDOBLER and WILSON, 1986). Histological examination has failed to reveal the presence in *B. manni* of special secretory cells that might contribute to the camouflage



Fig. 1. — Portion of a colony of *Basiceros manni* on their original nest material shortly after capture. Included are workers and larvae, the latter in various stages of growth. Note the remarkable camouflage of the workers.

Abb. 1. — Ein Teil einer Kolonie von *Basiceros manni* im natürlichen Nest. Arbeiterinnen und verschiedene Larvenstadien sind zu sehen. Beachte die bemerkenswerte Schutzfärbung einzelner Arbeiterinnen.

layer by the addition of either cryptically colored chemicals or adhesive substances that hold the soil.

The camouflage is improved still further by the exceptionally sparse and sluggish movements of the ants. When observed in an undisturbed state inside the chambers of an artificial nest, the entire worker force often stands perfectly still for minutes at a time. As illustrated by the data in *table II*, self-grooming is relatively uncommon. The *Basiceros* even hold their antennae rigid most of the time. 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. The overall result is that the ants are exceptionally difficult to distinguish against natural backgrounds.

Predation and diet

The *Basiceros manni* proved to be predators of small arthropods. The foraging workers walked with slow, deliberate movements, inspecting crevices and holes by inserting their wedge-shaped heads, sometimes pushing loose debris aside with the head, and antennating the surface. When a prey

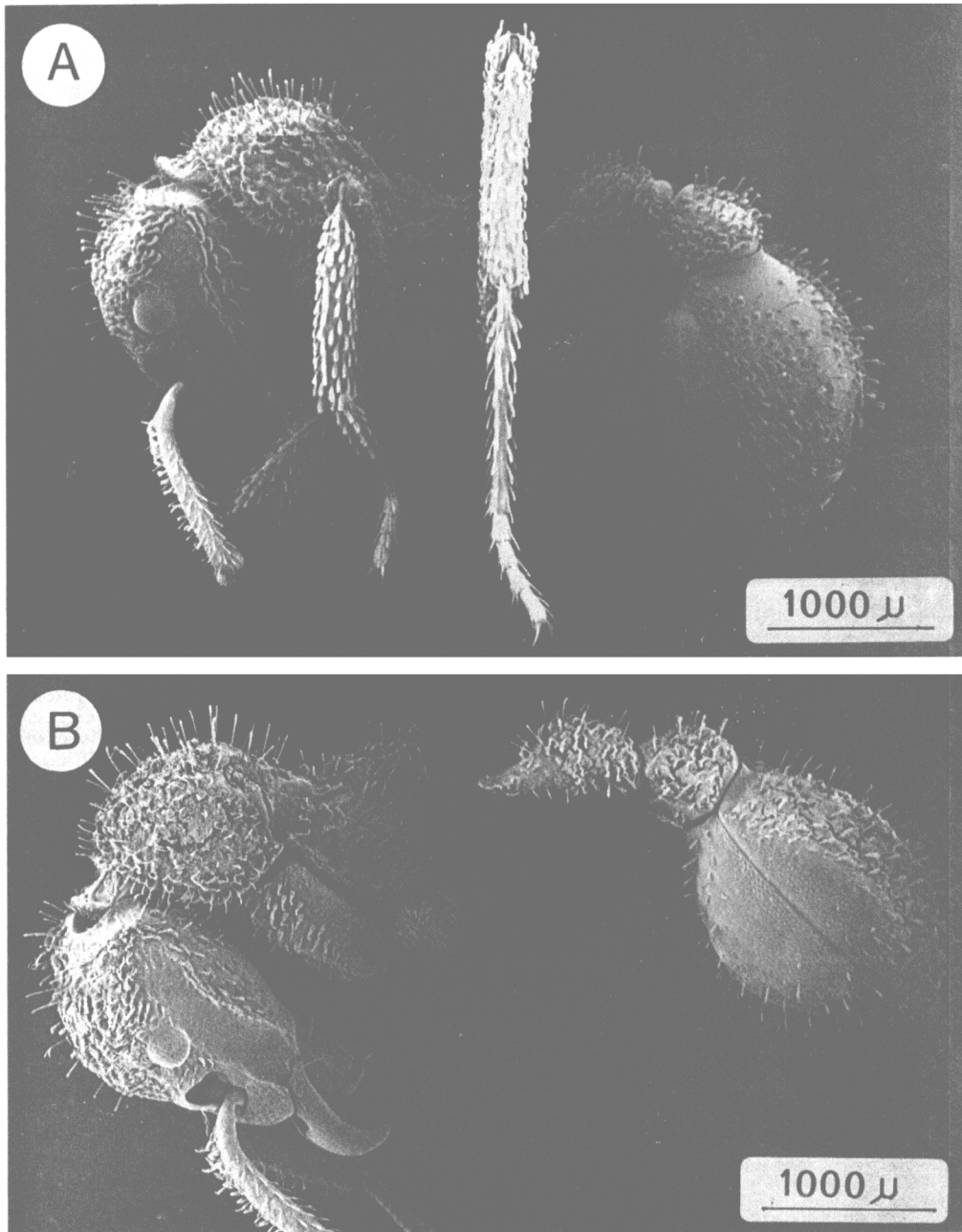


Fig. 2. — Lateral body views of *B. manni* workers (SEM photographs). *A*, a younger (shiny) worker with little or no soil accumulation; *B*, an older worker, which is fully encrusted with accumulated soil.

Abb. 2. — Seitenansicht von *B. manni* Arbeiterinnen (REM-Fotos). *A*, eine jüngere Arbeiterin (glänzend) mit keiner oder nur wenig Erde am Körper; *B*, ältere Arbeiterin mit einer dichten Erdkruste.

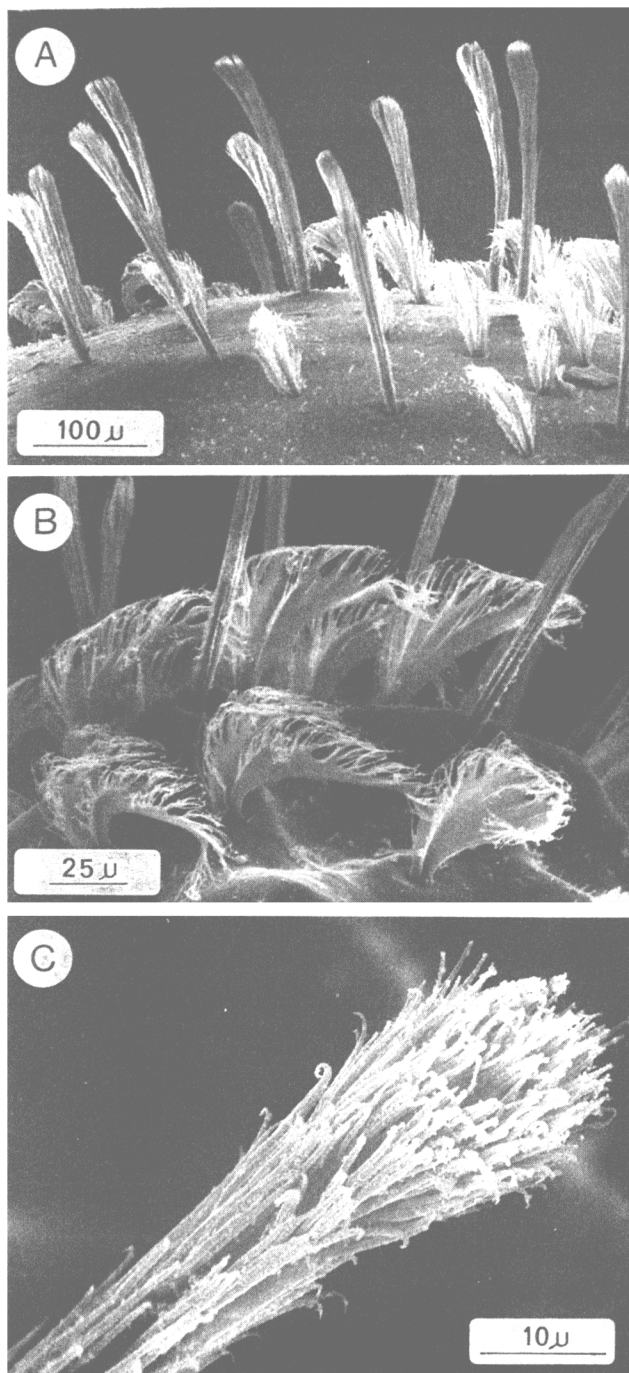


Fig. 3. — SEM photographs of body setae of *B. manni* workers. A, the characteristic 2-layer pilosity is illustrated in this view of the dorsum of the first gastric segment; B, a group of the lower, "feather" hairs is shown, in this case on the thoracic dorsum; C, the distal end of one of the longer, "brush" hairs on the thoracic dorsum.

Abb. 3. — REM-Aufnahmen von Haaren und Borsten am Körper von *B. manni* Arbeiterinnen. A, die typische doppelschichtige Behaarung auf der dorsalen Seite des ersten Gastersegmentes; B, die kleineren Federhaare auf der dorsalen Seite des Thorax; C, das obere Ende der längeren Pinselhaare auf der dorsalen Seite des Thorax.

object was encountered, the workers usually opened their slender, plier-shaped mandibles about 30 degrees and seized the prey without hesitation. A stinging motion followed immediately. When victims thrashed free at this point, the ants became much livelier, rushing back and forth over short distances in an attempt to seize the prey again. The venom was quite potent, taking effect from about 5 s to about a minute or somewhat longer. One centipede remained mostly paralyzed but still alive for a period of a full day.

The *Basiceros* evidently feed on a moderately wide range of small arthropods. We retrieved mostly consumed remains of two beetle larvae, one a possible cucujoid and another belonging to a different, unknown family (determined by Margaret THAYER), from the mandibles of a half-grown larva when the third nest was first discovered. In the laboratory at La Selva we offered mixed sets of the following arthropods in 4 "cafeteria" experiments, in which the ants were allowed to choose prey from a variety available from the vicinity of their nests in the field: small snails (2 species), isopods, spiderlings (several families), phalangids, amblypygids, millipedes (several families), geophilomorph centipedes, entomobryomorph collembolans, campodeid and japygid diplurans, lepidopteran thysanurans, hemipteran nymphs, zorapteran nymphs and adults, kalotermitid and nasutitermitine workers, earwig nymphs, cricket (grillid) nymphs, beetle larvae (3 families, including Ptilodactylidae), staphylinid and chrysomelid beetle adults, moth larvae and pupae (1 family), ant adults and brood (*Camponotus* sp.), and tabanid and chironomid fly adults. The ants readily accepted termite workers, a moth caterpillar, scarabaeid and elaterid-like beetle larvae, and centipedes. A zorapteran nymph was retrieved to the nest chamber, but its subsequent fate was not observed. The other organisms were consistently ignored. The ants appeared to accept termites more quickly than the other prey, but our records were too few and the conditions of the experiments too variable to permit a firm generalization. In the laboratory at Harvard the *Basiceros* colony thrived on *Drosophila* adults fed them as prey, rearing numerous brood over a period of 6 months.

Our findings are consistent with a single record by WEBER (1950) of a *B. singularis* worker carrying a dead termite in Guyana during the day, and the discovery by BROWN (1974) of 3 headless termites in the nest chambers of a *B. singularis* colony in northern Mato Grosso State, Brazil. BROWN also induced the colony to feed on crushed housefly pupae in the laboratory, and the workers reared two eggs to a mid-larval stage during 6 months.

Division of labor

We found it convenient to recognize four stages in coloration and accumulated body deposits that were correlated with age and hence useful in the study of temporal division of labor (see fig. 2, 4).

Callow. Freshly eclosed individuals that are light reddish brown in color; no body deposits, body surface fully shining.

Shiny. Fully colored (blackish brown), but with few or no deposits, so that the entire body surface is shining.

Partially encrusted. Crust patchily distributed over the dorsal body surface, leaving other patches shining.

Fully encrusted. Dorsal and lateral surface of entire body covered by a crust resembling a fine dark brown soil or mud deposit, which is broken by irregular cracks, evidently held together at least in part by dense pilosity, and can be easily scraped off with sharp forceps.

Table I. — Spatial distribution of "castes" in the nest: mean (\pm s.d.) number of workers in various locations during 5 snapshot counts taken at 30-min intervals.

Tabelle I. — Räumliche Verteilung der Kasten im Nest. Mittelwerte von 5 "Schnappschuss"-Zählungen (im Abstand von 30 Minuten) werden gegeben.

Activity	Callow	Shiny	Partially encrusted	Fully encrusted
Close to queen	0	2 \pm 2.3	2.2 \pm 1.6	4.8 \pm 2.6
Sitting away from brood	0.8 \pm 1.1	2 \pm 1.6	1.2 \pm 1.6	7.4 \pm 3.1
Sitting with larvae	0.4 \pm 0.7	5.8 \pm 0.8	4.6 \pm 1.1	1.4 \pm 1.1
Sitting with pupae	0.6 \pm 0.5	3.4 \pm 2.9	4.8 \pm 1.3	2.4 \pm 1.7
Walking in nest chamber	0	1.2 \pm 1.3	3.2 \pm 2.4	5 \pm 2.0
Walking in foraging chamber	0	0	0	1.4 \pm 1.1

There were striking differences in the physical location of these stages and the roles they performed (see *tables I, II*). In general, only the fully encrusted, hence older workers hunted in the foraging chambers, where they captured and retrieved prey. Inside the nest the shiny and partially encrusted (younger) workers took over the prey objects and brought them to the larvae, sometimes stinging the prey again. The younger workers often fed on the bodies of the prey simultaneously with the larvae, while the older ones typically dined alone well away from the brood. Furthermore, as shown in the tables, the younger workers were the primary brood attendants. Finally, in all three observed instances of adult carrying during colony emigration, the transporter was a fully encrusted worker. The proportions of workers of the several stages in the two colonies were as follows: in the first, 3 callow, 9 shiny, 11 partially encrusted, 21 fully encrusted; in the second, none callow, 14 shiny, 10 partially encrusted, 20 fully encrusted.

This temporal division of labor was accompanied by striking changes in ovarian development. We dissected 6 shiny and 6 fully encrusted workers from one colony, and found that the workers possess two ovarioles. Each of the shiny individuals had a single, mostly or completely full-sized egg in

Table II. — Behavioral repertoires of the three age stages of *Basiceros manni* workers (*shiny*, youngest; *partially encrusted*, middle-aged; *fully encrusted*, oldest) and the nest queen. The fractions given are those of each behavioral act within the repertoire of each of the 3 age classes. The full data were based on 6 hours of observation of the first of the two captive mature colonies.

Tabelle II. — Verhaltensrepertoire von drei Altersklassen von *Basiceros manni* Arbeiterinnen (*glänzend*, jüngste; *teilweise verkrustet*, mittleres Alter; *voll verkrustet*, älteste) und der Königin. Die Zahlenreihen geben den proportionalen Anteil aller beobachteten Verhaltensweisen innerhalb der 3 Altersklassen an. Diese Daten wurden während sechs stündiger Beobachtungen der ersten der beiden *B. manni* Kolonien gewonnen.

Behavioral Act	Shiny workers	Partially encrusted workers	Fully encrusted workers	Nest queen
Self-groom	0.021	0.007	0.007	0
Allogroom:				
callow adult	0.053	0	0.007	0
shiny worker	0.042	0.035	0	0
partially encrusted worker	0.016	0.035	0	0
fully encrusted worker	0	0.021	0.026	0
queen	0.128	0.084	0.066	0
Lick egg	0.043	0	0	0
Manipulate egg	0.080	0.056	0.026	0
Lick larva	0.202	0.168	0.033	0
Manipulate larva	0.069	0.098	0.026	0
Put prey on larva	0.064	0.063	0.007	0
Lick pupa	0.090	0.119	0.039	0
Manipulate pupa	0.069	0.070	0.053	0
Help eclosion of adult	0.027	0.014	0	0
Lay egg	0.011	0	0	0
Eat egg	0	0	0	1.000
Handle nest material	0	0.007	0.033	0
Attack prey and intruders	0	0	0.316	0
Handle prey inside nest	0.032	0.133	0.072	0
Feed on prey	0.048	0.056	0.092	0
Carry brood or nestmates during emigration	0.005	0.035	0.197	0
Total no. of observations	188	143	152	1
Total no. of categories observed	17	16	15	1
Estimated total no. of categories (mean \pm σ)	17 \pm 1	16 \pm 1	17 \pm 2	—

one or the other of the ovarioles, whereas none of the encrusted workers possessed eggs and their ovaries were furthermore considerably regressed. Two callows were found to lack eggs, while a single partially encrusted worker dissected had a small egg. In addition the poison gland reservoirs of the fully encrusted workers had volumes 2-3X those of the younger ants. We concluded that the greater ovarian development of the younger workers contributed to their role as nurses, in which they provided eggs for the queen and possibly for the larvae also, while the larger poison gland reservoirs of the older workers enhanced their abilities as the principal huntresses of the colony.

Queen size and behavior

An unusual feature of the colonies we collected is that the nest queens were approximately the same size as the average workers and were overall smaller than many of these individuals, exceeding them only in their more bulky thorax (*fig. 4*). In one of the two colonies measured, for example, the Head Width (maximum head width measured in full face) of the queen was 1.37 mm; that of 10 workers selected haphazardly ranged from 1.20 to 1.42 mm, with mean and standard error 1.37 ± 0.02 mm.

The queens were also singularly timid and inconspicuous, typically remaining hidden from view at the edge of the brood area or even well away from it. They escaped quickly when the nest was disturbed and showed no inclination to rescue brood. In each nest the queen was observed on single occasions to approach the brood pile and to eat an egg lying on the nest floor. Because workers were observed to lay eggs onto the floor on two occasions, we considered it likely that the egg eaten originated from a worker and hence was trophic in nature. A virgin queen was observed feeding directly on a termite worker lying in the brood chamber.

Trophallaxis

No instance of this behavior, so important in most other myrmicine ants, was observed during the study. During allogrooming workers were occasionally seen to be vigorously licking the mouthparts of nestmates, perhaps in response to the presence of the scent of prey. The movements could easily be mistaken for liquid food exchange, but did not include the true movements of the latter behavior, which include the persistent application of the glossae, opening of the donor's mandibles and closure of the recipient's mandibles, the play of the recipient's antennae around the glossae, and (often) the presence of a visible droplet of liquid.

Emigration

A total of 3 emigrations were induced in the two mature colonies of *Basiceros manni* by the simple expedient of placing them in the exposed

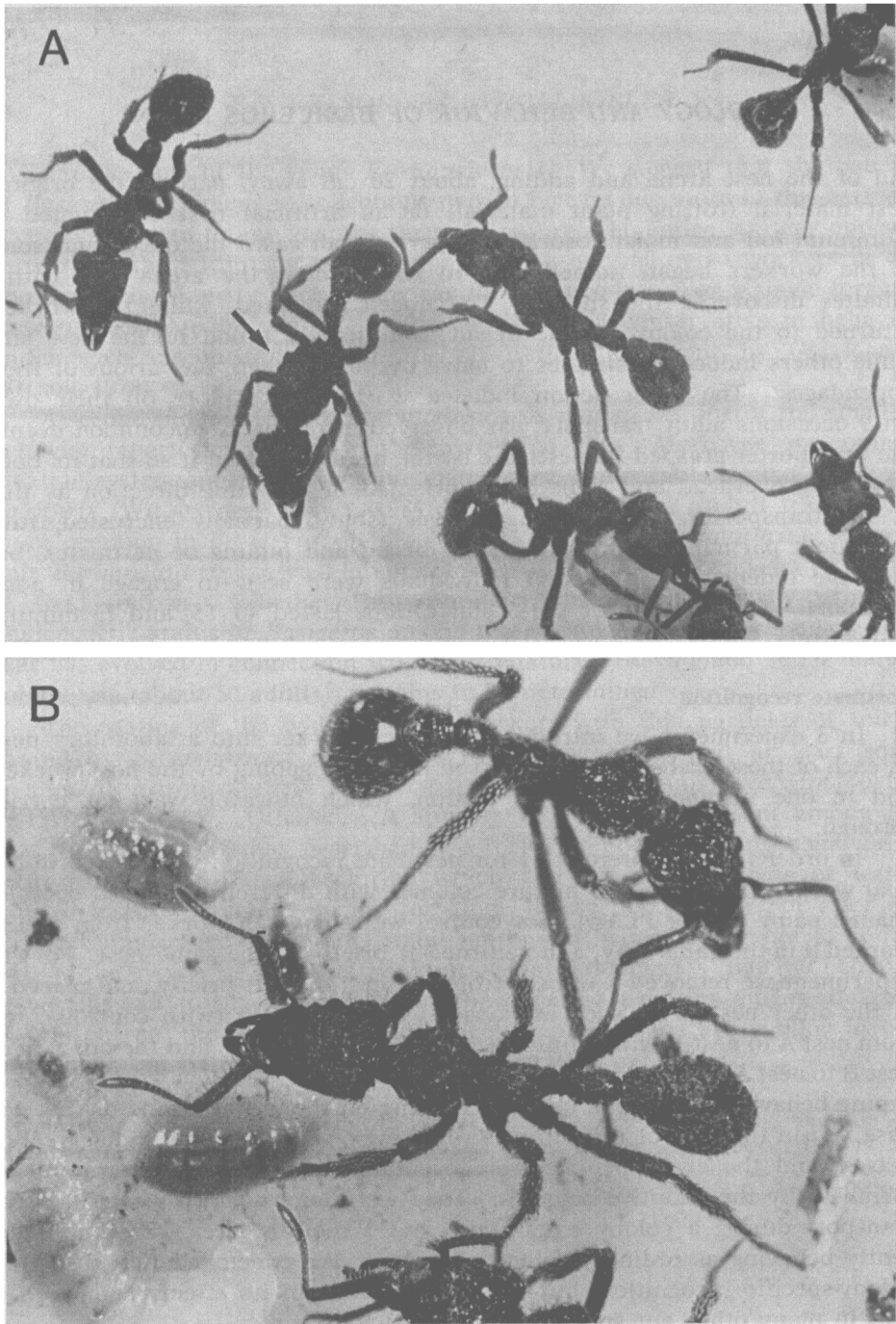


Fig. 4. — Views of living *B. manni* adults. *A*, the nest queen (indicated by arrow) with a group of workers; in this photograph, the queen is characteristically untended. *B*, a younger, shiny worker (*above*) is contrasted with an older individual, which is fully encrusted with fine soil.

Abb. 4. — Kasten der *B. manni*. *A*, die Königin (Pfeil) mit einer Gruppe von Arbeiterinnen. *B*, eine jüngere, glänzende (*oben*), und eine ältere, verkrustete Arbeiterin (*unten*).

end of the nest arena and adding, about 20 cm away, part of the original nest material (rotting plant material) or an artificial nest constructed of aluminum foil and moist absorbent paper. In all cases the queen and some of the workers began immediately to roam about the arena and within minutes discovered the shelter. The queen remained, while the workers returned to the colony. Some began to transport brood to the new site, while others induced nestmates to move by pulling them on various of their appendages. The latter action induced workers to explore on their own. On 9 occasions adult transport was observed, a relatively uncommon event: the transporter grasped its nestmate by the head and lifted it so that its body was slung overhead and came to be oriented in the same direction as that of the transporter. All three age stages (shiny, partially encrusted, fully encrusted) participated in transport of brood and pulling of nestmates, but only the older, fully encrusted individuals were seen to engage in adult transport. The duration of the 3 emigrations lasted 40, 55, and 75 minutes respectively.

Nestmate recognition

In 3 experiments we introduced an alien worker into a laboratory nest. In each of these exchanges we observed mandible gaping by the host workers and in one instance a stinging motion, which however was not carried through.

In order to test more closely for nestmate recognition we marked individual workers from the two mature colonies with differently colored spots of enamel paint (Testor PLA®). For control we removed a worker from a nest, marked it in the same way, and returned it briefly to the same nest. For the experiment we removed a worker from the nest, held it briefly, and placed it in the other nest. Two such exchanges were conducted (with controls), one from nest A to nest B with a fully encrusted (older) worker, and the other from nest B to nest A with a shiny (younger) worker. Again, the alien workers evoked gaping behavior and in one instance nipping on the gaster; none of this was observed in the case of the controls. However, after 1-2 mins the aggression ceased, and the experimentals were eventually accepted as apparently full members by the adoptive colonies. They were later seen to assist in brood transport during a colony emigration, and 3 months later were still apparently behaving as ordinary colony members. We concluded that there is a colony-specific recognition, but one that is weak in its effects compared to that in many other ant species.

DISCUSSION

The *Basiceros* are even more sluggish and cryptically colored than *Smithistruma* and other dacetine ants, as well as the more closely related

basicerotine ants of the genus *Eurhopalothrix*. We suggest that the paucity of *Basiceros* specimens in collections may in fact be due more to this extreme cryptobiosis than to any genuine rarity in nature. The entire strategy appears to work to the advantage of the colony. With only 50 or so workers in the population at maturity, each colony can ill afford to lose even a single forager. It would seem to be adaptive to be cautious and conservative in behavior under such circumstances (see the theoretical argument by OSTER and WILSON, 1978).

A second notable feature is that *Basiceros manni* has one of the smallest behavior repertoires known in the myrmicine ants. Moreover, its communication system appears to be quite elementary, comparable to that of *Eurhopalothrix* (WILSON and BROWN, 1984). But details differ: adult transport is more common in *Basiceros* (it is nearly absent on *Eurhopalothrix*), whereas only *Eurhopalothrix* (at least larger colonies of *E. heliscata*) appears to recruit to food sources. Whether this simplicity reflects a basically primitive phylogenetic status of *Basiceros* among the Myrmicinae, or a secondary trait that has evolved in connection with its predatory behavior and small mature colony size (about 50 adults), remains to be determined.

The coating of the body of older workers with fine particles of soil is shared by *Stegomyrmex connectans* (Stegomyrmecini) and at least some species of *Eurhopalothrix* and *Octostruma* (Basicerotini) (see HÖLLDOBLER and WILSON, 1986). Otherwise it appears to be rare or absent among the ants. MASUKO (1984) has described two forms of body-smearing behavior in short-mandibulate Dacetini, during which workers acquire coats of water, soil, or insect excrement during foraging. These deposits do not alter the physical appearance of the ants significantly and hence appear not to contribute to the avoidance of visual predators. Masuko suggests that the behavior serves instead to mask the odor of the dacetine workers during stalking. If this is true, the basicerotine and dacetine phenomena are similar in outward form but basically different in function.

ACKNOWLEDGMENTS. — We are grateful to Robert M. FAGEN for estimating the total number of behavioral categories from our data (tables I, II), and to Kathleen M. HORTON and Ed SELING for important assistance in the preparation of the manuscript and SEM figures. Research was supported in part by National Science Foundation grants BSR-84-21962 (WILSON) and BNS-82-19060 (HÖLLDOBLER).

References

- BROWN W.L., 1974. — A supplement to the revision of the ant genus *Basiceros* (Hymenoptera: Formicidae). *J. New York Entomol. Soc.*, 82, 131-140.
BROWN W.L., KEMPF W.W., 1960. — A world revision of the ant tribe Basicerotini. *Studia Entomol.*, 3, 161-250.
FAGEN R.M., GOLDMAN R., 1977. — Behavioural catalogue analysis methods. *Anim. Behav.*, 25, 261-274.

- HÖLLDOBLER B., WILSON E.O., 1986. — Soil-binding and camouflage in basicerotine and stegomyrmecine ants (Hymenoptera: Formicidae). *Zoomorphology*, in press.
- MASUKO K., 1984. — Studies on the predatory biology of Oriental dacetine ants (Hymenoptera: Formicidae). I. Some Japanese species of *Strumigenys*, *Pentastroma*, and *Epitritus*, and a Malaysian *Labidogenys*, with special reference to hunting tactics in short-mandibulate forms. *Ins. Soc.*, 31, 429-451.
- OSTER G.F., WILSON E.O., 1978. — *Caste and Ecology in the Social Insects*. Princeton Univ. Press, Princeton, N.J.
- WEBER N.A., 1950. — New Trinidad Myrmicinae, with a note on *Basiceros* Schulz (Hymenoptera, Formicidae). *Am. Mus. Nov.*, no. 1465, 6 pp.
- WILSON E.O., 1957. — Feeding behavior in the ant *Rhopalothrix biroi* Szabó. *Psyche* (Cambridge), 63, 21-23.
- WILSON E.O., BROWN W.L. Jr., 1984. — Behavior of the cryptobiotic predaceous ant *Eurhopalothrix heliscata*, n. sp. (Hymenoptera: Formicidae: Basicerotini). *Ins. Soc.*, 31, 408-428.
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