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Insectes Sociaux, Paris
1984, Volume 31, n° 4, pp. 408-428

BEHAVIOR OF THE CRYPTOBIOTIC PREDACEOUS ANT *EURHOPALOTHRIX HELISCATA*, N. SP. (HYMENOPTERA : FORMICIDAE : BASICEROTINI)

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Reçu le 17 avril 1984. Accepté le 23 juillet 1984.

SUMMARY

1. *Eurhopalothrix heliscata* n. sp. is an Asiatic representative of the little known ant tribe Basicerotini and the first member of the group to be studied intensively. We report evidence that it preys on a variety of termites, but also takes at least some other kinds of insects. Overall, the social behavior is simple relative to that of many other myrmicine ants.

2. Prey are hunted and retrieved singly. But foraging workers are also able to recruit nestmates to the vicinity of groups of prey and as a result accelerate retrieval of termites to the brood chambers. A prolonged exploration of the surrounding area also ensues.

3. With the aid of chemical cues, workers are able to recognize material from the vicinity of their nest.

4. The workers are notably thigmotactic. They use their wedge-shaped heads, hard bodies, and short legs to press into tight spaces. They seize the appendages of termites with their short, sharp-toothed mandibles, clasping these body parts of the prey even more tightly with the aid of their projecting, heavily sclerotized labra.

5. *E. heliscata* tend to gather in large, broodless groups away from the main part of the colony. This bivouacing behavior, which effectively dispenses the foragers over a wider area, may improve the efficiency of the predation on termites.

6. The workers appear not to practice food exchange, worker oviposition, or alarm-defense behavior, nor do they recruit during colony emigration.

7. Prolonged fighting and dominance-subordinance relations among queens have been observed under laboratory conditions.

8. Other details of nesting behavior and social interactions are described (see, *e.g., table I).*

ZUSAMMENFASSUNG

Verhalten der kryptobiotisch-rauberischen Ameise Eurhopalothrix heliscata **n. sp. (Hymenoptera, Formicidæ, Basicerotini)**

1. *Eurhopalothrix heliscata* n. sp. ist eine asiatische Vertreterin des wenig bekannten Ameisen-Tribus Basicerotini. Es ist die erste Angehorige dieser Gruppe, die genau unter-

sucht wurde. Es erbeutet Termiten, nimmt aber auch einige Insekten als Beute an. Im Vergleich zu vielen anderen Myrmicinen ist ihr soziales Verhalten einfach.

2. *E. heliscata* ist eine Einzeljagerin. Wenn mehrere Beuteobjekte gefunden werden, konnen Arbeiterinnen Nestgenossinnen rekrutieren ; das beschleunigt das Eintragen der Beute. Das fuhrt oft auch zu einer ausgedehnten Erkundung der weiteren Umgebung.

3. Arbeiterinnen erkennen chemisch Material aus der Nahe ihres Nestes.

4. Die Arbeiterinnen sind bemerkenswert thigmotaktisch. Mit ihren keilformigen Kopfen, harten Korpern und kurzen Beinen drucken sie sich in enge Raume. Mit ihren scharfgezahnten Mandibeln ergreifen sie die Extremitaten der Termiten und sie packen die Beute noch fester mit ihren stark sklerotisierten Labra.

5. *E. heliscata* versammeln sich oft in Gruppen, ohne Brut und weg von der Hauptkolonie. Dieses Bivouac-Verhalten, das die Furagiere über eine weitere Flache verteilt, scheint der Termitenjagd gut angepasst zu sein.

6. Futteraustausch, Eier legende Arbeiterinnen, Alarm-Verteidigungsverhalten und Rekrutierung wahrend Nest-Emigration wurden nicht beobachtet.

7. Im Labornest kampfen die Koniginnen haufig miteinander und zeigen ausgepragtes Dominanzverhalten.

8. Weitere Einzelheiten zum Nest- und Sozialverhalten werden beschrieben (siehe *Tabelle I).*

INTRODUCTION

The ant tribe Basicerotini comprises *Basiceros, Rhopalothrix, Eurhopalothrix,* and five other genera, and is a group of approximately sixty known species limited primarily to tropical forests in the New World and Indo-Australian region. In spite of its wide distribution, it is one of the rarest and least known assemblages of tribal rank. As shown by BROWN and KEMPF (1960) in their monographic revision, basicerotines have the expected anatomical characteristics of cryptobiotic and predaceous ants. They are small- to medium-sized, possessing a thick, hard integument, often flattened head shape, and broad, deep scrobes that receive most or all of the antennae. The scapes are dorsoventrally depressed, and in some species their basal angles form prominent anterior lobes. The ants also possess greatly reduced maxillary and labial palps, a prominent and heavily sclerotized labrum, and solidly fused pro- and mesonota. The pilosity is typically bizarre : much of the body is covered by hairs that are clavate, spatulate, globose, or some other unusual shape. Additional details of anatomy and classification have been added by TAYLOR (1968, 1970, 1980) and BROWN (1980).

The workers are cryptic in appearance and unusually sluggish in their movements. They freeze and feign death by rolling into a pupal posture at the slightest disturbance, and hence are unusually difficult to find during routine collecting efforts. Only a few colonies have been located over years of collecting, and few data are available on them. In a study of the Papuan *Eurhopalothrix biroi,* WILSON (1956) found that the workers prey on a wide variety of soft-bodied arthropods, which they capture by careful stalking and

convulsive snaps of their sharp-toothed mandibles. Only a few observations on the social behavior of *E. biroi* could be made under the field conditions then prevailing.

Recently a large colony of an undescribed species of *Eurhopalothrix* was collected by Mark Moffett at Singapore and transported in good condition to Harvard University, where we were able to make a more prolonged and leisurely study than has hitherto been possible for any basicerotine species. The ants were kept under almost daily observation for a period of six weeks. In the account to follow, which goes well beyond the earlier report on *biroi*, we begin by providing a formal taxonomic description of the species, then proceed to a systematic account of its natural history with special reference to behavior. A full behavioral repertory is given in *table I*, while behavioral categories of special interest are discussed separately.

Table I. — The behavioral repertory of the laboratory colony of *Eurhopalothrix heliscata*. The true number of behavioral categories was estimated by fitting to a lognormal Poisson distribution (see FAGEN and GOLDMAN, 1977).

Tabelle I. — Das Verhaltensrepertoir der Labor-Kolonie von *Eurhopalothrix heliscata*. Die wahre Zahl der Verhaltens-Kategorien wurde geschätzt durch Anpassung an die lognormale Poisson Verteilung (siehe FAGEN und GOLDMAN, 1977).

Behavioral category	No. acts observed	Behavioral category	No. acts observed
Self-grooming	203	Forage	126
Allogroom adult :		Capture prey	112
Minor worker	10	Carry prey to and inside nest	65
Dealate queen	2	Feed on prey inside nest	195
Alate queen	13	Lick and manipulate meconium	4
Brood care :		Carry dead larva	3
Carry or roll egg	34	Carry dead adult nestmate	4
Lick egg	16	Handle nest material and detritus	19
Carry or roll larva	71	Antennal tipping	1
Lick larva	95	Drag dealate queen	2
Feed larva solid food	11		
Carry or roll pupa	8	TOTAL	1 000
Lick pupa	6		

No. behavioral categories observed = 21.

Est. no. behavioral categories ($\bar{x} \pm$ s.e.) = 21 ± 2.

Eurhopalothrix heliscata new species
(fig. 1-3)

Worker, holotype (Bukit Timah, Singapore): TL 4.4, HL 1.02, HW 1.12 (CI 110), ML 0.25 (MI 25), SL 0.61 (SI 54), EL 0.05, WL 1.20, petiole L 0.42, postpetiole L 0.41, hind femur L 0.76, hind tibia L 0.54 mm. [Measurements and indices as in BROWN and KEMPF, 1960: 167-170; L is length, W is width, I is index; cephalic index (CI) is head W (HW) × 100/head L (HL); mandibular index (CI) is mandibular L (ML) × 100/HL; scape index (SI) is scape L, measured from apex of basal lobe to apex of scape × 100/HW; EL is maximum eye L; WL is diagonal L of trunk in side view.]

Worker, composite description based on 98 specimens from the type locality and from Sungei Menyala Reserve, Malaysia, mainly compared with workers of *E. procera* from 5 localities in the Philippines.

Measurements from 5 individuals in the Bukit Timah and Sungei Menyala series, including the largest and smallest of 44 checked: TL 4.0-4.7, HL 0.94-1.06, HW 1.02-1.19 (CI 109-114), ML 0.23-0.29 (MI 24-27), SL 0.56-0.64 (SI 54-55), EL 0.04-0.06, WL 1.12-1.31, petiole L 0.39-0.46, postpetiole L 0.34-0.42, hind femur L 0.70-0.82, hind tibia L 0.53-0.70 mm.

1. Eyes smaller than in *E. procera,* deeply sunken into the dorsolateral cephalic margins, and with fewer ommatidia (estimated at 12-15 in 50 X stereomicroscope view; more than 15 ommatidia in *E. procera). E. procera* has EL usually $>$ 0.06 mm.

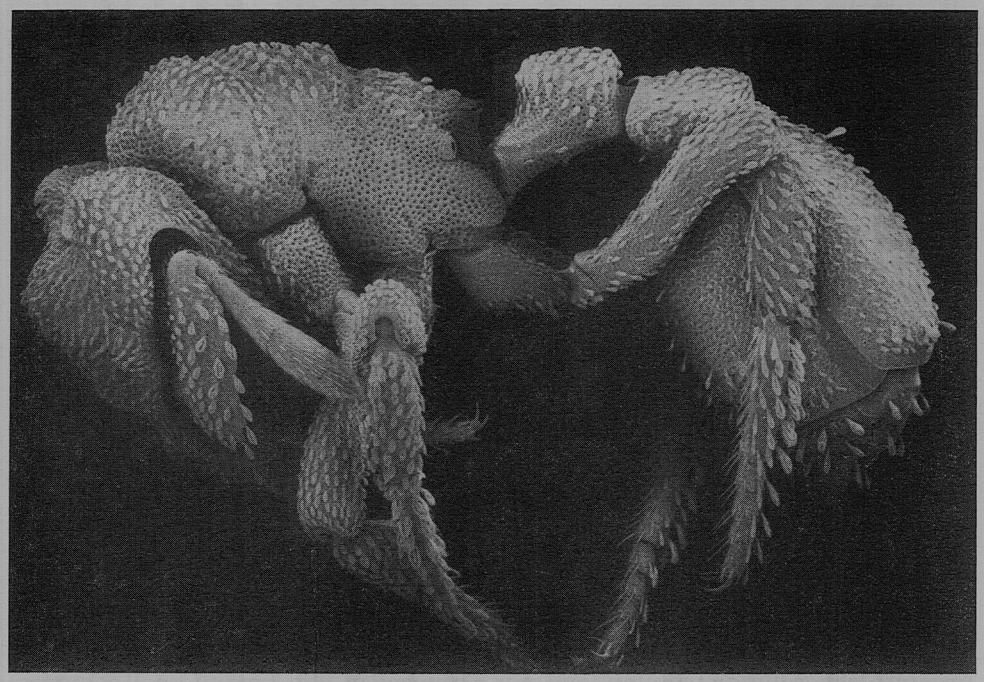
2. Ground hairs throughout, but especially on gastric dorsum, more conspicuous, thicker, and slightly more distinctly decumbent, raised above the integumental surface. On gaster, the difference between the small ground hairs and larger, suberect specialized hairs is less pronounced than in *E. procera,* and the larger hairs are relatively shorter and thicker (flattened-clavate or inverted spoon-shaped), more abundant (18-26 on first gastric tergum), generally distributed, and not arranged in two longitudinal columns framing a more sparsely liveried median strip, the condition in most *E. procera.* Six of the larger hairs tend to form a circlet around the apical margin of the first as well as the succeeding three apical gastric segments.

3. Sculpture of body opaque in general, punctulate areas densely and coarsely so, with no shine over lower pleura. On gastric dorsum, punctulae very dense and coarse, subcontiguous, on disc of first segment, 20 or less per 0.1 mm square (more in *E. procera,* due to the relative fineness of the punctulae in that species), with extremely narrow interspaces which, however, are often weakly shining despite the overall opaque surface effect. Minute denticles, seen at some views on the ventral petiolar keel of *E. procera* from the Moluccas and eastward, are absent in *E. heliscata,* as in most western samples of *E. procera.*

4. Color deep reddish brown.

Additional character states of possible significance include the absence or weak differentiation in *E. heliscata* of the larger, specialized "humeral" hairs on the pronotal tumuli. Also, in *E. heliscata,* the petiolar node appears to be more quadratic in side view, but this is partly an illusion based on the greater development of the posterodorsal pilosity.

Worker prepupae from M-171 were prepared for karyotyping according to the method of IMAI *et al.* (1977), and brain tissue was examined from four individuals, all of which gave some readable chromosome spreads. More than 60 spreads were examined at length, and nearly all of these yielded diploid counts of 18 metacentric and submetacentric chromosomes, with a few tetraploids at 36 chromosomes *(fig. 3).* As is common in such studies, a few



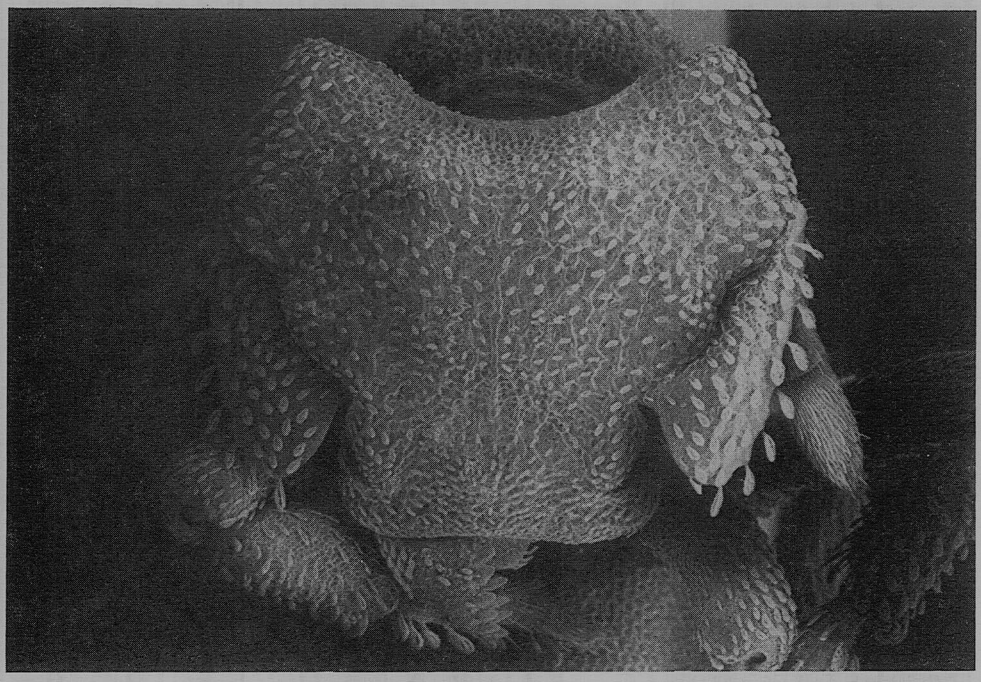


Fig. 1. — Paratype worker of *Eurhopalothrix heliscata*. *Upper*, side view of entire body. *Lower*, frontal view of head, with left mandible removed to reveal the projecting, sclerotized labrum.

Abb. 1. — Paratypus der Arbeiterin von *Eurhopalothrix heliscata*. *Oben*, Seitenansicht der Ameise. *Unten*, Vorderansicht des Kopfes. Der rechte Kiefer wurde entfernt, um das hervorstehende sklerotisierte Labrum zu zeigen.

Fig. 2. — Paratype worker of *Eurhopalothrix heliscata,* dorsal view.

Abb. 2. — Paratypus der Arbeiterin von *Eurhopalothrix heliscata,* dorsale Ansicht.

random spreads showed chromosome totals below the usual 18 or 36, probably because one or more chromosomes had been lost from the nucleus during preparation, or were covered by another chromosome. In deducing the haploid set of 9 chromosomes, we can distinguish two large submetacentrics and a remaining series of seven, graded downwards in size to one or two metacentrics that are 1/3 to 1/2 as long as the largest members of the set. This is the first karyotype reported for any species of the myrmicine tribe Basicerotini.

Queen, alate, Bukit Timah (one measured of four examined): TL 5.3, HL 1.10, HW 1.21 (CI 110), ML 0.29 (MI 26), SL 0.67 (SI 55), EL 0.20, WL 1.45, petiole L 0.50, postpetiole L 0.47, forewing L 4.24 mm.

Male: Three specimens from Bukit Timah; one measured: TL 4.2, HL 0.73, HW including eyes 0.80, ML 0.15, SL 0.16, EL 0.27, WL 1.35, petiole L 0.49, postpetiole L 0.32, forewing L 3.6 mm. Readily distinguished from *procera* males originating from Palau and Solomon Islands by the coarser, deeper punctulae (in both species the entire body is punctulate) and shorter, proportionately thicker hairs.

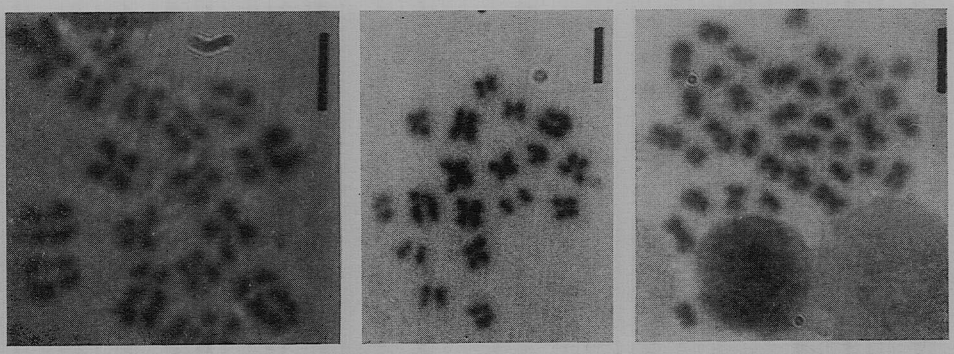


Fig. 3. — Representative chromosome complements of *Eurhopalothrix heliscata* n. sp. from brain of worker prepupa (three different individual insects) *ex* colony series M-171 from Sungei Menyala Reserve, near Port Dickson, Malaysia. Left and center frames: diploid spreads, 2n = 18 metacentrics and submetacentrics (M). Right frame: tetraploid spread, 4n = 36. Scale bars in each case equal 2 micra.

Abb. 3. — Chromosomensatz von *Eurhopalothrix heliscata* n. sp., entnommen vom Gehirn einer Präpuppe (drei verschiedene Insekten) der Kolonie M-171 von Sungei Menyala Reserve, nahe Port Dickson, Malaysia. Links und in der Mitte: diploide Verteilung, 2n = 18; Rechts: tetraploide Verteilung, 4n = 36. Masstab entspricht 2 microns.

This species belongs to the *E. procera* superspecies, which ranges from Samoa and Fiji, extending westward through Melanesia, Palau Islands, and the Cape York Peninsula of Australia to the Philippines, Botel Tobago Island, Borneo, and now, the Malayan Peninsula. As Brown and Kempf showed in 1960, *E. procera* itself displays a rough centrifugal cline centered on New Guinea, where sculpture and pilosity are relatively reduced, to the extremes of the range both in the Pacific and toward the West, where sculpture and pilosity tend to be coarser and more widely present over the body. Of course, most of these populations occur allopatrically and disjointly, so there is no guarantee that they are all conspecific. Indeed, on some larger islands, mostly near the Pacific range periphery, phenetically distinct populations appear to have budded off the ancestral *procera* stock as species (*cinnamea* on Manus Island, *szentivanyi* and *hoplites* on New Guinea, *greensladei* and *isabellae* in the Solomons, *emeryi* and *insidiatrix* on Fiji). *E. heliscata* may represent the western counterpart of the eastern within-*procera* variants, but its characters seem to us so extreme a development of the peripheral traits, particularly the reduced worker eye size, that we have designated it as a species separate from *E. procera*. This decision eventually may be reversed in favor of including the Malayan populations in *E. procera*, but in the absence of adequate samples of the complex from the Greater Sunda Islands, the recognition of *E. heliscata* as a separate species appears to be the most prudent decision.

It should be noted that our analysis of the *E. procera* variation includes

two new single worker samples, one from Seram in the south Moluccas (above Hararu, about 150 m in forest, near Masohi on the South Coast), HW 1.10 mm, color piceous, sculpture and pilosity near typical *E. procera* (collected by W.L. Brown) ; and one from the Air Madidi Slope of Mt. Klabat, N. Sulawesi, in rotten wood of rain forest (also collected by Brown). The latter worker is small (HW 1.00 mm) and reddish brown, but is so encrusted in foreign material that details of sculpture and pilosity are obscured. (We can also report a considerable range extension for *E. szentivanyi,* based on a nest series taken in rotten wood in wet hill forest south of Vanimo, West Sepik District, in extreme northwestern Papua New Guinea, collected by BROWN. See also the recent reports by TAYLOR, 1968, 1970, 1980).

The name *heliscata* is taken from the diminutive of the Greek word *helos,* a nail or stud, and implies "mini-studded" in reference to the peculiar pilosity of the new species.

The holotype and part of the paratype series are in the Museum of Comparative Zoology, Harvard University. Other paratypes have been placed in the British Museum (Natural History) ; the Australian National Insect Collection, C.S.I.R.O. (Canberra, Australia) ; and Cornell University Insect Collection.

CULTURING METHOD

The Singapore *Eurhopalothrix* colony was housed in an artificial nest designed for soil- and log-dwelling ants by one of us and used extensively in studies of the genus *Pheidole* (WILSON, 1984). A plaster of Paris bed 1 cm deep was laid in the bottom of a clear plastic box 24 × 32 cm (the dimensions can be increased or decreased according to the size of the colony). Galleries and chambers similar in dimensions to those of the original nest in the field were carved into the plaster surface at one end of the bed, and the network was covered by a glass plate. In addition, some of the original nest material or litter and soil from the nest vicinity was scattered on the exposed part of the floor to increase the "naturalness" of the laboratory environment. Finally, the inner sides of the box were lined with Fluon (Northeast Chemical Co., Woonsockett, R.I.) or talc (Mallinckrodt, St. Louis) to prevent escape of foraging workers.

RESULTS

Nest and colony composition

The Singapore colony was found in a large piece of red rotting wood (62 × 26 cm) half-buried in the soil of rain forest. Large numbers of workers, reproductive forms, and brood were concentrated in a complex network of clean galleries and chambers that ranged in diameter from about one to ten millimeters. Upon arrival in the United States this sample contained 424 workers, 26 alate queens, 6 dealate queens (some or all of which might have been recently dealated within the nest), 8 males, 5 larvae in various stages of development, and 10 eggs (see *fig. 4).* In the original collection, Mark Moffett observed many more males and brood pieces in all stages of

development, scattered through small, clean chambers in the rotting wood. In another rotting log 3.5 meters away, Moffett found an additional group of approximately 100 workers unaccompanied by brood or reproductive forms. The ants were restricted to an area of about a square meter, dense in some spots but not clumped.

The Malaysian colony (M-171) was found on 27 March 1981, at Sungei Menyala Forest Reserve, near Port Dickson, Negeri Sembilan, in mature lowland forest by Tho Yow Pong and W.L. Brown. The nest was dispersed through one end of a large, red-rotten log lying in deep shade. This *Eurhopalothrix heliscata* colony was a large one like the first, containing hundreds (certainly more than 200) of workers and abundant brood, but no queen was found in the time available for search. A living part of the nest population was brought away in a jar, together with some of the termite heads, for laboratory observation. Both adult workers and larvae were seen to continue feeding on termite heads in the manner described while housed in an artificial nest.

Fig. 4. — Portion of the living colony of *Eurhopalothrix heliscata* shortly after capture, with dealate and alate queens, workers, and larvae in view. (Photograph by Bert Hölldobler).

Abb. 4. — Teil der lebenden Kolonie von *Eurhopalothrix heliscata* kurz nachdem sie gefangen wurde, mit entflügelten und geflügelten Königinnen, Arbeiterinnen und Larven (Foto : Bert Hölldobler).

Foraging and prey capture

Like other basicerotines observed in life, the *Eurhopalothrix heliscata* workers moved at an unusually slow and deliberate pace, stopping frequently to stand quietly for varying periods of time. In comparison with other ants we have observed in life they were highly thigmotactic, pressing readily into tight spaces and moving inwardly as far as possible. Here their peculiar body form served them well: their wedge-shaped heads with retractable antennae could be thrust into tiny crevices, while their hard bodies could be squeezed under low ceilings by the pulling and extension of the relatively short, thick legs. Sometimes the exertions resembled swimming movements, with the legs being pulled to the side and backward repeatedly to gain short forward movements of the body. It was our impression that the foraging workers were acting rather like miniature ferrets. They seemed to be specialized to some extent for hunting in places not ordinarily visited by ants of comparable size.

E. heliscata feeds to a substantial degree on termites. This generalization is suggested first of all by the observations of Mr. Moffett in the field. When he opened the log containing the broodless segment of the colony at Bukit Timah Reserve, he encountered a number of covered trails of *Odontotermes* sp. crisscrossing the zone occupied by the ants. One of the workers captured a worker termite and carried it away as he watched. The kitchen midden collected next to the main colony (with queens and brood) contained the remains of hundreds of termites belonging to a wide range of genera: *Bulbitermes* (2-3 species), *Havilanditermes, Odontotermes,* and *Macrotermes.* In addition, there was part of the exoskeleton of a small polydesmid centipede, possibly adventitious. Strangely, there were no apparent remains of *Homallotermes foraminifer* or *Parrhinotermes* sp., the two species nesting in the same log as the *Eurhopalothrix,* or of the *Eurhopalothrix* themselves.

Comparable observations were made by Tho and Brown on the Malaysian colony. Adjacent to and above the *Eurhopalothrix* nest in the log was an equally diffuse nest of the larger, black, ponerine ant *Pachycondyla leeuwenhoeki,* in which were found scattered headless bodies of large worker termites (*Odontotermes* sp.). Living termites of the same species were abundant in galleries elsewhere in the log. The large, shiny, orange heads of the termites were found scattered through the *Eurhopalothrix* nest chambers. Several of the *E. heliscata* larvae were apparently feeding singly on several of them by extending head and neck through the foramen magnum of the termite cranium. No postcranial remains of termites, or parts of other arthropods, were found in the *Eurhopalothrix* nest, and it seemed evident that the termite heads must have been obtained from the *Pachycondyla* after the latter had bitten them off. A few stray workers of *E. heliscata* were found wandering in the *Pachycondyla* chambers and galleries, and indeed it appeared that the runways of the two nests anastomosed in a few places.

Thus *E. heliscata* appear to be generalized termite feeders. But at least under some circumstances, they also prey on other kinds of insects, in the manner reported earlier for *E. biroi* (WILSON, 1956). When the fragments of rotting wood containing the Bukit Timah Reserve colony were broken apart in the laboratory at Harvard University, a small group of workers with two larvae were found clustered on and around a beetle larva (possibly an elaterid). The ant larvae were positioned on the larva in a characteristic feeding position. Thereafter the ants readily captured and fed on both *Nasutitermes corniger* and flightless mutants of *Drosophila melanogaster*.

The following account of predatory behavior is based on more than a hundred observations of the capture and transport of prey in the laboratory nest, primarily of *Nasutitermes*. The workers appeared to become aware of the prey only when they closed to within 3-4 mm. Sometimes they avoided the insects after making contact, simply backing off or turning aside to continue walking at the same leisurely pace. More often they moved toward the insect slowly, sometimes after a pause of five to ten seconds, while playing their antennal funiculi forward. The mandibles were opened to full or nearly full extent, so that the masticatory borders were separated by a distance 80-90 percent the width of the clypeus and at a slight angle from their base. With a convulsive snap the ant then seized the appendage, usually far enough back along its own masticatory border so that as the mandibles closed the appendage was also pressed on one side or the other by the labrum.

When seized in this manner the insect usually struggled violently. In most cases the ant then held its original approach position, with the body fully extended, and waited for a few seconds. It next lifted the prey up slightly by raising the forward part of its own body while simultaneously curling its abdomen beneath its thorax and head to sting the prey.

As the leg or antenna was seized and the prey reacted, the ant retracted its own antennae. Now the function of the peculiar antennal form became apparent. The funiculus, containing most of the delicate sensilla, was wholly protected beneath the broad flange of the scape. The scape itself was pulled in medially to slide part of the way into the deep antennal scrobes. In this position it seemed almost fused to the armored head surface.

The escape attempts of the prey were sometimes so powerful that the attacking *Eurhopalothrix* lost its footing, and the ant was either dragged a short distance — or else predator and prey tumbled briefly through somersaults while remaining locked together. Sometimes the ant let go at this point, but more often it held on long enough to subdue the prey. (The sting of the *Eurhopalothrix* is relatively long; when the abdomen was cut off, causing reflex stinging, it extruded about 0.3 mm beyond the tip of the abdomen and thus appeared capable of penetrating deep within the body of the prey.) After five to ten minutes, most of the fruit flies and termites became quiet, presumably paralyzed by the venom, and the ant proceeded

either to carry them in a forward movement or else to drag them backward towards the brood chambers. During transport the *Eurhopalothrix* extended their antennae fully once again.

Recruitment

It was discovered that the workers of *Eurhopalothrix heliscata* recruit efficiently over short distances to food finds. When only one or two *Drosophila* adults or *Nasutitermes* workers were placed in the foraging arena, they were captured and retrieved haphazardly by individual foraging workers; and no noticeable build-up of *Eurhopalothrix* followed. But when ten or more such prey were made available — and especially if they were first immobilized and grouped in a single spot — there was a dramatic increase of workers foraging in the arena, ordinarily 5 X or more over the original force, within a period of 15 minutes (see *fig. 5)*.

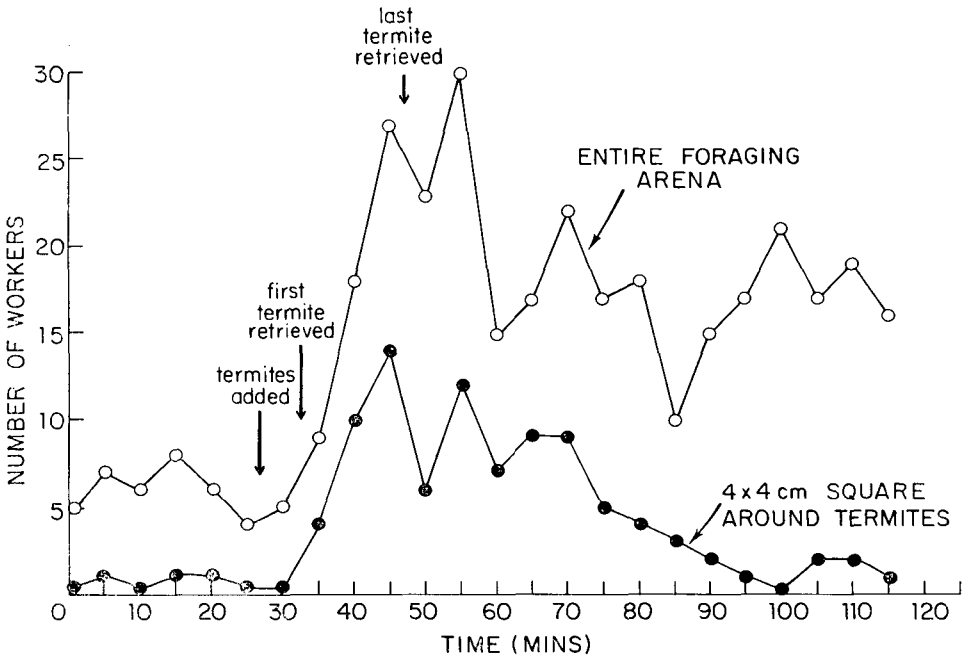


Fig. 5. — The buildup of foraging workers of *E. heliscata* in the foraging arena of a laboratory nest following introduction of a group of 20 *Nasutitermes corniger* workers and soldiers. The termites were placed inside a 4 × 4 cm space near the nest entrance. Even after the termites had all been captured and retrieved, and the target square was mostly abandoned, a substantial force of workers continued to patrol the arena as a whole.

Abb. 5. — Die Zunahme futtersuchender Arbeiterinnen von *E. heliscata* in der Arena des Labornestes, nachdem eine Gruppe von 20 *Nasutitermes corniger* Arbeiterinnen und Soldaten geboten wurden. Die Termiten wurden innerhalb eines 4 × 4 cm grossen Quadrates in der Nähe des Nesteinganges ausgelegt. Selbst nachdem alle Termiten eingetragen waren, erkundete immer noch eine grössere Schar von Arbeiterinnen die weitere Arena.

Although we had the impression from this evidence that a weak chemical trail might be used in recruitment to prey, at least for short distances, we were unable to substantiate its presence with further experimentation. We laid artificial trails from just inside the nest for 15 cm out across the arena floor, using three replicates each of the following body parts crushed onto the tips of sharpened hardwood applicator sticks : the posterior third of the abdomen, Dufour's gland, poison gland, hind gut, and all tissue in the terminal segments remaining after the last three parts had been removed, the entire head, and the entire alitrunk. The results were uniformly negative : no tracking occurred. However, the absence of trail-following under these artificial conditions, without reinforcement of possible auxiliary signals or stimuli from newly captured prey, cannot be regarded as disproving the presence of a chemical trail.

Regardless of the nature of the signal used, the recruitment was clearcut in execution and effective. It resulted in rapid concentration of a substantial force of workers at the termite piles, with many more fanning out to patrol the remainder of the arena. The latter phenomenon, that is, the searching in the vicinity, was greatly enhanced by the low degree of precision in the recruitment process in the first place, such that many foragers missed the termite pile altogether and continued searching around and beyond it. This pattern of recruitment is remarkably similar to that described by HÖLLDOBLER (1981) for the predaceous dacetine ant *Orectognathus versicolor*. An interesting feature of the *Eurhopalothrix* response was that long after all of the termites had been retrieved, during an hour or more, a large force of workers continued patrolling the arena.

Orientation

A principal remaining problem in the study of cryptobiotic ants generally is the means by which they orient back and forth to the brood chambers, through complex three-dimensional passageways and without the aid of light. In the experiments to be reported below, we found that the workers are, at the very least, able to distinguish paper kept next to the brood chambers from blank controls, an ability that could aid substantially in homing.

In two replicates, pieces of filter paper 6 × 12 cm were laid along the floor of the foraging arena next to the entrances to the brood chambers, and the workers were allowed to walk and rest on them for 3 days. Then sections 4 × 4 cm were cut out, crumpled into a wad, and placed into one of ten 8-mm-wide holes drilled at equally spaced intervals into the side of the wall of a circular plexiglass arena 7.5 cm in diameter. The hole in which the paper was placed was selected randomly. At the same time identical but untreated wads of paper were placed into the remaining nine holes. The ends of the wads were bent down to touch the surface of the arena so that each formed a miniature shelter. In five replicates each using this procedure, five

Eurhopalothrix workers were placed in the center of the arena, which was then covered with a glass plate to reduce air currents and drying. A single light was placed directly overhead and the rest of the room darkened, thus eliminating visual cues. In each replicate the compass direction of the hole containing the paper from the *Eurhopalothrix* nest was changed at random. The ants were given 15 minutes to explore the arena, and their locations were noted.

In all of the five trials 2 to 4 of the *Eurhopalothrix* workers settled on the wad from near the brood chambers, and in only two replicates a single worker settled on a control wad ; the remaining workers were still wandering over the arena floor. The probability that a group of workers would choose any one of the ten wads for all of the $n = 5$ trials by chance alone, as did happen in this case, is $10^{n-1} = 10^{-4}$. The actual total numerical distribution of workers (18 on the experimental wad, two on all of the remaining 9 wads) is even more statistically significant. We concluded that the workers recognized some chemical cue from the vicinity of their nest chambers, with at least sufficient acuity to distinguish it from blank controls.

The apparent absence of trophallaxis and trophic eggs

Although a special effort was made to detect liquid food exchange during more than ten hours of observation, none was seen between adults or between adults and larvae. Nor was any sign of trophic egg production observed. Insofar as could be determined both the adults (including the queens) and the larvae obtained all of their nourishment by feeding directly on prey items. However, the matter is not entirely closed : we were unable to observe the care of first-instar larvae, which conceivably might receive liquid food or eggs. Another curious circumstance was that feeding was limited to the nest chambers. We saw no instance of workers consuming freshly captured prey while they were still in the foraging arena.

Age polyethism

Eurhopalothrix heliscata, like all other known basicerotines, is monomorphic, and division of labor by the existing small amounts of isometric size variation was apparently nonexistent. At least a simple form of age polyethism did occur nonetheless. Workers that were light in color and with the least amount of grayish deposit on their dorsa — hence clearly the younger individuals — were seen associated with the brood at a frequency much higher than their representation in the colony as a whole, standing over the larvae and eggs, grooming them, and sometimes carrying them to new positions in the nest chambers. They were assisted in these simple tasks by darker, more heavily incrusted, and presumably older workers. On the other hand, only older workers were observed foraging and retrieving termites.

Emigration and adult transport

Three episodes of emigration across the arena floor were recorded. In the first, we placed the colony soon after its capture on the open floor and observed the adults as they found their way into the more secure, shaded artificial brood chambers located along one end of the arena. In the second, the colony was exposed completely by the removal of the glass plate and the progress of the adults recorded as they moved across a sheet of moistened absorbent paper to shelters on the other side. In the third, all of the adults were gathered up with their brood and recently captured termites, deposited as a group in the center of the papered floor, and observed as they found their way back to the newly covered and darkened artificial brood chambers.

In the case of similar experiments performed with most other species of ants (see for example HÖLLDOBLER, 1981), any one of the above procedures triggers well-marked recruitment to the nest site and is often accompanied by adult transport. In the case of the *Eurhopalothrix*, however, we could detect no trace of organized movement or recruitment. The workers and queens simply moved out on their own in irregular, looping paths, coming to settle — and clump together — in the nearest protected sites. Many individuals carried brood and previously captured termites with them, and some made what appeared to be return trips to transport additional burdens. But no sign could be detected of trail laying or consistent following of any particular pathway. Eventually individual workers from some groups discovered those in others, and the aggregations grew in size over a period of hours until most of the colony had reassembled in the brood chambers or other favored sites.

During all of this rather chaotic activity we saw only one instance of adult transport : a well-colored (hence older) worker was observed carrying another worker by the waist. The transportee was waving its legs awkwardly in the process. In other words it did not respond in the typical formicid fashion by assuming a passive pupal posture.

Brood care

The eggs were quite large relative to the worker body size, about the size of the entire mandibular blade of a worker, or 0.3 mm long and 0.2 mm wide. There were 10 to 40 present during most of the observation period. They were kept in one to three tight heaps. These piles were covered at all times by the bodies of resting workers, which were predominantly light colored and with clean dorsal exoskeletons — in other words, presumably young adults. The larger larvae and pupae were scattered in variable-sized groups through the brood chambers. They too were usually partly covered by quiescent groups of mostly younger attendants. As indicated in the repertory data of *table I*, all of the brood stages were licked and carried about

at moderately frequent intervals, although it was our clear impression that they were attended much less frequently than in the case of other, more active myrmicine ants such as species of *Leptothorax, Pheidole* and *Solenopsis.*

The larvae were transported in a distinctive manner reminiscent of prey retrieval. That is, the workers did not usually grasp the bodies of the larvae directly in their sharp teeth but instead gripped one or more of the abundant hairs that projected from all sides of the body. They then either lifted the larvae off the ground and carried them in a forward walking movement, or else — in the case of some of the larger larvae — dragged them while walking backward. The ants were relatively indifferent to the exact position of the hairs they seized, although in most cases they utilized hairs on the back or sides of the larva. Thus in a series of 60 episodes recorded, involving quarter- to full-grown larvae, the hairs gripped by transporting workers were on the dorsum 22 times, on one side or the other 31 times, and on the venter 7 times. The position of the hairs utilized also ranged widely, from just behind the head to the tip of the abdomen. In 5 cases some part of the body itself was held during transport.

The morphology of *Eurhopalothrix* larvae suits them very well for this atypical form of transport. As noted by WHEELER and WHEELER (1954, 1960), their bodies are densely covered by erect hairs, many of which are relatively long and curved at the tip. In the case of *E. bolaui,* some of the hairs have swollen tips. It is quite easy for workers to get a firm grip from almost any direction.

The *E. heliscata* workers fed the larvae by placing entire prey or fragments of prey directly on top of them or next to them. The larvae were very active, in a manner reminiscent of those of *Myrmecia* and many ponerines. They turned and stretched the anterior parts of their body frequently and sometimes for considerable distances, changing the positions of their heads by as much as half their full body lengths. These maneuvers enabled them to reach and feed on many prey items placed next to them that otherwise would have been unattainable. Occasionally larvae convulsed the entire length of their bodies, causing them to roll completely over. The maneuver resulted in a slight shift of location, sometimes up to a body length from the original location, but there was no evidence of a sequencing of such movements that resulted in a consistent locomotion across the brood chamber floor.

Defense

Eurhopalothrix are among the most exquisitely camouflaged of all ants, at least to the human eye. In shape, size and color their bodies closely match the particles of rotting wood and soil among which they live. The effect is enhanced by the slow, deliberate movements of the workers and their tendency to rest motionless for long periods of time in crevices and beneath sheltering

objects when away from the nest. Workers uncovered freeze in position for a minute or longer. When disturbed mechanically, as by the touch of a pair of forceps, they feign death by crumpling into a ball-like pupal posture, from which they emerge into renewed activity only if left alone for several minutes. When the nest cover is broken open, the ants inside are very difficult to see, and we suspect this would cause difficulties for birds, lizards, or other visually orienting predators. Thus we were able to extract the entire Singapore colony only by gradually drying out their nest material and removing groups of individuals concentrated in moist retreats, one by one, following close inspection.

The *Eurhopalothrix* adults were also remarkably passive when threatened by natural enemies. When minor workers of two species of *Pheidole* were introduced into the *Eurhopalothrix* foraging arena in the laboratory, the inhabitants responded by ignoring or avoiding them. We then forced the issue by grasping live, struggling *Pheidole* workers in the tips of forceps and presenting them to *Eurhopalothrix* workers located on the foraging arena and just inside the nest entrance. Usually the basicerotines just backed away to a safe distance. Sometimes they froze into immobility, retracting their antennae in the same manner as when attacking prey, and in a few instances they opened their mandibles as though to strike. On one occasion, out of 40 such presentations, a *Eurhopalothrix* seized a *Pheidole* worker by the leg but (unlike the treatment of *Drosophila* and *Nasutitermes* offered in the same manner, which were attacked as prey) the basicerotine did not attempt to sting, and it soon let go with no visible harm to the intruder. On these various occasions no sign of alarm was observed among nestmates close by, either around the nest entrance or further back in the brood chambers.

Fighting among queens

When the colony was first established in an artificial nest, both alate and dealate queens were present. Oviposition occurred continuously afterward, with eggs increasing in number from 10 to over 50 within a month. Within a day after the colony had settled in new quarters, fighting was observed between a pair of dealate queens. Battles were seen in progress almost continuously thereafter for a week; they then became increasingly intermittent and finally ceased altogether. On several occasions two pairs were locked in combat at the same time, and at various times either fully dealate or partly (but never fully) winged individuals were engaged. We inferred that at least five individuals were involved on different days, and the total number during the 17-day period may have been far higher. However, not all interactions were aggressive. Most of the time queens simply moved on past when they encountered each other, and on two occasions a dealate queen was observed grooming another.

In a typical aggressive episode the two individuals were locked together

like wrestlers, with one trying to maintain a hold on the body of the other with all her legs while her opponent struggled to escape. Sometimes the aggressor rolled her own body around the head and anterior portion of the opponent's alitrunk; on other occasions she centered her attack on the alitrunk, and occasionally farther back, on the gaster. Typically the aggressor pressed her mandibles downward and against the body of the opponent, evidently to gain added purchase. Several times we saw one queen biting an antenna or portion of the vertex of the opponent. In most episodes the aggressor also pressed the tip of her gaster against the body of her adversary in an additional attempt to gain better purchase. We saw no evidence of stinging at this time, although the sting could easily have been extruded periodically and into the body of the adversary without being seen.

In most instances one queen was clearly dominant and the other subordinate. The dominant attempted to hold the subordinate in place, while the subordinate either struggled to work free or else lay quietly in a ball-like " pupal " posture. Several times the two appeared to be more evenly matched, so that neither could get a commanding position on top of the other. In both cases the combatants jockeyed and rolled around sluggishly for up to 15 minutes or longer. In one case three queens rather than two fought together briefly; one then walked away and left the struggle to the remaining pair.

Subordinates that managed to break free usually walked briskly a short distance from the scene. One was seen to depart from the brood chambers to the outer nest chambers, only to return after a few minutes — and suffer another attack. There was one piece of indirect evidence that damage was being inflicted during the battles. The mortality of the queens was much higher than that of the workers, the reverse of the usual case in ant colonies. By the end of the 17-day period during which fighting occurred, the number of queens dropped from 25 to 5. During this entire time no episodes of aggression were witnessed among workers or between workers and queens.

Kitchen midden

A well-formed kitchen midden, consisting primarily of the remains of termites, was found by Moffett near the main nest chambers in the field at the Bukit Timah Reserve, Singapore. The workers constructed another in the laboratory nest, at the far corner of the foraging arena on the opposite side of the foraging area from the brood chambers.

Mating

A single male survived for several days in the laboratory nest. On 10 December 1983, we saw two alate queens repeatedly approach him in one of the brood chambers, antennating his body closely. They also climbed partly on top of him several times. No workers were seen to behave in this fashion toward the male, or toward any other nest member. On the next day

the male was found attempting to mate with an alate queen inside one of the brood chambers. While pressing against her right side, he gripped her wings and gaster with his legs and pressed the tip of his gaster against hers.

DISCUSSION

The anatomical and behavioral specializations of *Eurhopalothrix heliscata* fit together in a manner that increases the efficiency of foraging. The workers have a strong propensity to force their bodies into tight spaces. Their combination of thick integument, tapered head shape, scale-like pilosity, and short, stout legs enhances the ability to forage in this manner. Similarly, the short mandibles and relatively narrow mandibular gape, well suited for hunting in narrow spaces, is complemented by the row of sharp teeth arrayed along the entire masticatory border and the heavily sclerotized, protruding labrum that presses against objects seized by the ants. The *Eurhopalothrix* appropriately direct their strike not against the bodies of prey (at least not those of termites and other insects their own size) but against appendages.

A curious trait of the *E. heliscata* workers is their propensity to settle in groups and rest for prolonged periods of time away from the brood chambers. We note that this pattern enhances the effectiveness of predation against termites. The basicerotines are solitary huntresses that do not rely on mass raiding as in the case of some species of *Leptogenys, Megaponera,* and *Pachycondyla.* They are able to recruit nestmates, but the communication is relatively short-range and imprecise. It is therefore of advantage for colonies with these traits to possess staging areas from which forays against termite colonies can be conducted over relatively short distances whenever workers discover foraging columns of the insects or breaks in their nests. The prey items can then be transported at a more leisurely rate back to the brood chambers. Such a relay system was in fact maintained by the laboratory colony, although they operated it across a much shorter distance than is evidently the rule in nature.

The behavioral repertory proved otherwise remarkably limited for a myrmicine ant, lacking as it does liquid food exchange (at least among adults and between adults and larger larvae), trophic eggs, or any organized form of food retrieval, alarm communication, and defense. We do not interpret the absence of these traits as necessarily constituting primitive qualities. After all, *Eurhopalothrix* and other known basicerotines are quite advanced in many anatomical characters. Rather, the reduced behavioral repertory appears to be associated with the mostly solitary hunting techniques and cryptobiotic habits of the species, among the latter of which is defense based on cryptic coloration, slow movements, and the feigning of death. We suggest that the reduced repertory is itself a derived trait in evolution. The dis-

tinction can be examined further when a better understanding of the phylogenetic position of the Basicerotini is secured, including more information on the behavior of the nearest phylogenetic out-groups.

Finally, the fighting among queens is an interesting discovery on its own. We know of no comparable case in the ants, although it is common enough among polistine wasps and bumblebees. In ants supernumerary queens are often eliminated by the workers, as revealed in studies of *Crematogaster, Solenopsis, Plagiolepis,* and *Myrmecocystus* (see WILSON, 1971 ; BARTZ and HÖLLDOBLER, 1982). Unfortunately, we do not know the full circumstances that led to the prolonged conflict within the *Eurhopalothrix* colony. We could not learn whether inseminated nest queens were involved, nor were we able to establish the origin of the participants : whether they were nestmates by birth or came from other colonies and joined this one after their nuptial flights.

In conclusion, while this study of *Eurhopalothrix heliscata* has substantially increased knowledge of the Basicerotini, research on this obscure group is still in a very early stage. The life cycle and colony structure of *Eurhopalothrix* are still imperfectly understood, and the natural history of other genera, including *Basiceros* itself, remains almost wholly unexplored. A challenging task of the future is to gain information on enough basicerotine species to work out the elementary evolutionary trends in foraging behavior and prey selection, as has already been accomplished for the independently evolved tribe Dacetini (BROWN and WILSON, 1959 ; WILSON, 1962).

ACKNOWLEDGMENTS. — We wish to thank Mr. Mark MOFFETT for supplying the colony of *E. heliscata* from Singapore from which the holotype and behavioral studies were drawn. D.H. MURPHY, of the Zoology Department, National University of Singapore, assisted in the collecting and also helped to identify the termites associated with the ants. We are also grateful to Dr. THO YOW PONG, of the Forest Research Institute, Kepong, who arranged W.L. BROWN's trip to Sungei Menyala Reserve and joined him in the collecting effort. Facilities of the Department of Genetics, University of Malaya, were opened to BROWN by Prof. YONG HOI SEN and departmental technician Rosli SARJAN. Much of the later chromosome searching was done by Frank RAMBERG and Eric WIENER, and they also took and processed (along with Thomas EISNER) the photographs of the *E. heliscata* karyotype. The research was supported in part by National Science Foundation grant BSR 81-19350 to WILSON and DEB 80-03722 to BROWN.

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