ARTHROPODS ASSOCIATED WITH NEOTROPICAL ARMY ANTS WITH A REVIEW OF THE BEHAVIOR OF THESE ANTS (ARTHROPODA; FORMICIDAE: DORYLINAE)

by

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This dissertation is not to be considered as published in its present mimeographed form. It contains many manuscript names for species and other taxa, and none of these should be quoted in any publication until the descriptions have been published. Included in this dissertation are manuscript names by the following authors: Cross, Dodge, Rettenmeyer, and Snyder.

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I. INTRODUCTION

This paper summarizes the known fragments of biological information for the arthropods which have been found with the Neotropical Dorylinae. In addition, new observations are included on the behavior of the ants and associated arthropods in Panamá and Kansas. Papers about arthropods associated with the Neotropical army ants have been published steadily since 1887. These studies have been limited almost exclusively to taxonomic treatments of specific families or groups of insects. The noninsectan arthropods have been largely ignored, and there has been little attempt to compare or integrate the knowledge of one group of insects with that of another. Information on the numbers of myrmecophiles living within the colonies of any species of army ant is almost universally lacking. Moreover, statements concerning the biology of all the myrmecophiles have been primarily opinions and speculation with no sharp lines drawn between these and biological facts. Most of the literature written about the arthropod guests was published before any serious studies had been made on the biology or behavior of the ants themselves. Now, after the extensive work by Schneirla and his co-workers, it is possible to try to integrate the behavior of the arthropods with that of the army ants.

Although other ants show varying degrees of nomadism and group-raiding, the term army ants has been used almost exclusively for members of the subfamily Dorylinae. In this paper the term army ants refers to members of the tribe Ecitonini, the main group of Neotropical army ants. In addition to having different morphological characters, army ants differ from other ants because of a combination of behavioral characters. The outstanding features of their behavior are: (1) they feed almost exclusively on animal prey which is collected by large groups of raiding workers; (2) the raiding groups are usually connected to the nest by at least one continuous column; (3) the entire colony periodically and frequently emigrates to new nest sites; (4) emigrations are largely dependent on the size, caste, age and range of ages of the brood (or broods)[1]; and (5) colonies are founded by division of an entire colony into two (or possibly several) daughter colonies. Although other ants may possess some of the above characteristics, apparently none possesses all of them. Moreover, a colony of army ants has a very large number of workers but usually only a single queen except at one time of the year when new queens are produced. Colonies usually have over 50,000 workers and may have over 1,000,000.

Most of the work by Schneirla has been concentrated on the species Eciton hamatum and burchelli which have a distinct activity

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[1] The term "brood" follows the usage of Schneirla (1949b: 7, etc.) which is different from the common use of the term when referring to other social insects. The eggs of most species of army ants are laid in large numbers in a relatively short period of about ten days, separated by periods of about two or three weeks in which no eggs are laid. As a result, the immature stages from each batch of eggs are approximately the same age within a colony and are referred to as a brood (or synchronous brood). Colonies can have two distinct broods at one time if the development of one brood lasts long enough to overlap partially a second. Where all developmental stages are found simultaneously within the same colony, the brood will be referred to here as a nonsynchronous brood.

cycle of alternating nomadic and statary phases. This cycle is diagrammed in figure 63 which indicates how the nomadic and statary phases and other behavior of the ants are correlated with the ages of broods. Schneirla has not written a summary paper giving the aspects of army ant behavior which are most useful for a discussion of the myrmecophiles. Therefore, a review of this work will be given here along with some new observations and minor differences in interpretations. The behavior of <u>Eciton</u> <u>hamatum</u> will be discussed first in some detail, since this species has been most extensively studied, and its behavior comes closest to a diagrammatic "textbook example" of the army ant activity cycle. Following this, the behavior of other species of army ants, primarily from Panamá and Kansas, will be discussed in less detail with emphasis on differences from and similarities to the behavior of <u>E</u>. <u>hamatum</u>.

Working with army ants is rather different from studying most other ants, and few descriptions of applicable methods have been published by Schneirla. Experience has shown that these methods, though simple, are not obvious. Consequently, this paper includes a section on methods for collecting and studying the army ants and the arthropods associated with them.

Preserved samples of approximately 800,000 workers and larvae were examined for myrmecophiles, and samples of at least 200,000 living workers were examined in the laboratory in Panamá. These samples came from about 200 colonies including those from 63 colonies sampled by other collectors at various localities. A summary of the numbers of workers, larvae and colonies is given in tables 3 and 4. All samples listed in these tables were counted completely except for ones with eggs and young larvae. The number of samples including more than 50 and 100 adult workers are also given.

DISTINGUISHING ARMY ANTS FROM OTHER ANTS IN THE FIELD

Since many other species of ants can be found in columns or clusters, it is important to be able to distinguish the army ants, or tribe Ecitonini, in the field. For this purpose, a combination of morphological and behavioral characters is most useful.

Most army ant workers are under eight millimeters in length; and therefore, many species of ants, including species commonly killed by army ants, are larger than the dorylines. Sometimes people hesitate to collect army ants, because the ants have a reputation for having severe stings and bites. The fierce reputation of army ants is based almost exclusively on the behavior of only three of about 140 species. Even though workers of all species have stings, these are too weak to puncture human skin in most cases. The largest species of army ants, those of the genus <u>Eciton</u>, with workers up to 14 millimeters long, have fairly weak stings. The majors or largest workers of all species of <u>Eciton</u> (except <u>rapax</u>) have disproportionately large, hooked mandibles, which inflict painful bites. However, it is possible to collect and study these ants readily without receiving any stings or bites, and they are not nearly as hazardous to work with as the honeybee. Many nondoryline ants of comparable size have bites or stings which are more severe than those of the Ecitonini.

The workers of both <u>Eciton</u> and <u>Labidus</u> exhibit a great amount of polymorphism. <u>Eciton</u> workers range in length from four to 14 millimeters. <u>Labidus</u> workers range from two to 13 millimeters, and the largest workers have disproportionately large heads, but the mandibles are not long and hooked as in Eciton. Neivamyrmex workers range from two to six millimeters in length, and Nomamyrmex workers, from three to 12 millimeters. However, in the latter two genera, the size range within any one species is more limited, and there is little allometry with respect to head size.

The compound eyes of all the workers of Ecitonini are reduced to a single pair of external facets which look like ocelli except for their lower and more lateral position. The eyes of the smallest workers are further reduced to a spot in the integument without a distinct convex cornea, or the eyes may be completely absent. None of the workers has ocelli. If facets can be seen on the surface of an eye of a worker ant, the ant is not an army ant. In addition, the petiole of the workers consists of two segments approximately equal in size and shape; the frontal carinae do not extend over the bases of the antennae; the legs are relatively long, and on the under surface of the hind tibia there is a lighter-colored stripe or elongate spot.

Army ant colonies are frequently found by hunting for columns of ants running along the ground. With practice, one can distinguish these ants from other ants in most cases by the quick manner in which they run. Their legs are long, and the ants run quickly and steadily in distinct columns without many workers deviating from the trail. There are few or no workers standing still, unless the column is a strong emigration column and guard workers are present. As the ants run, the antennae are held in front of the head and curved close to the ground as in figures 1, 9 and 10. The abdomen is also kept close to the ground and never is turned up at the tip or turned over the thorax. Sometimes "guard" workers may stand at the edges of the column with their front legs off the ground as in figure 11. In this position, they normally have their mandibles open and their antennae extended above their heads. These workers can be found anywhere in a column, but usually are where the workers are especially disturbed or excited, such as at the edges of emigration columns. They may indicate the position of the queen or a nest.

All objects which the Ecitonini carry are held *under* their bodies. This behavior will distinguish these ants from many others, especially the leaf cutters. (See figures 5, 6, 7, 9 and 10 of *Eciton burchelli* carrying worker larvae and booty.) A few species will occasionally eat nutmeats, vegetable oils or fruit. However, if large numbers of ants are seen carrying leaves or other plant parts, the ants are not Ecitonini. If army ants are carrying anything, it almost invariably is part of an arthropod and most commonly is the brood of ants or wasps. The Ecitonini do little digging and if they transport dirt, it is only for a few centimeters.

The ability to distinguish whether the brood is that of army ants is of major importance for distinguishing emigration from raid columns and thus for finding bivouacs. Fortunately, no species of army ant is known to carry off the brood of any other species of army ant. Therefore, if the brood is all the same approximate age and there is a considerable amount of brood, it is almost certain to be that of the army ant species carrying it. The army ants usually carry their own larvae by grasping the thoracic segments, whereas ant larvae which are booty are frequently carried by the posterior ends. The army ant brood seen is usually all larvae, but there may be cocoons with mature pupae in them along with young larvae and eggs. There may be large larvae and some cocoons with larvae or prepupae in them. It would be extremely unusual to see pupae being carried at the middle stage of their development, since at that time the colony is normally statary. Only in colonies of the genus Labidus can one find brood of all ages at the same time.

In addition, the larvae of Ecitonini have a characteristic appearance. Detailed descriptions of several species have been published by G. C. Wheeler (1943). The larvae are relatively long and slender with a curved, more narrow anterior end (see figures 22, 23, and 26a). They have heads which are larger or about the same size as the segments to which they are attached, unlike many ant larvae which have relatively much smaller heads. The larvae are entirely white and covered with inconspicuous setae, and there are no tufts or much longer setae among the pile-like covering. Although the larvae are usually approximately the same age, there may be a fairly large range in size among the more polymorphic species. The genus Neivamyrmex has pupae which are not enclosed in cocoons, but the genera Eciton, Labidus and Nomamyrmex have cocoons. If a column of army ants is transporting brood of another species of ant, this brood most frequently varies more in size and age; and parts of adult ants or entire dead ants which are carried often appear to be the same species as the carried pupae. Rarely a raid column of army ants can be found in which several hundred larvae of one species of ant prey are being carried. However, these will appear in a group preceded and followed by army ants without booty or with different booty. If the larvae are those of the army ants, there will be thousands of them, and they will be carried along an emigration route for a period of several hours.

Among the dorylines only the males have wings, but these wings normally drop off after the males have flown from their parent colony. Most males are collected at lights where one may wish to distinguish them from other male ants. Since some males lose their wings at lights, one should look around on the ground below a light for dealate males. The males range from about seven to 23 millimeters in length. As a rule, they are about twice the length of the largest workers of their species. All Neotropical doryline males have a similar appearance and are quite easy to distinguish from other male and queen ants. Their color varies from yellow-brown or orange, to dark brown, red-browns or black. They have large mandibles, large compound eyes and three large ocelli. The large eyes and ocelli will readily distinguish dealate males found in columns from queens, since the queens have eyes similar to those of the workers. The head is attached low on the thorax and is often hidden under it in dorsal view. The thorax is elongate or rectangular in dorsal view, not spherical. The strongly curved dorsum of the thorax and the low position of the head give the males a humpbacked appearance. There is a distinct constriction between the propodeum and the petiole. The petiole consists of a single large segment which frequently lacks the distinct dorsal node found in most ants, but may have a pair of large lateral nodes. Moreover, the petiolar segment is often so large and closely appressed to the gaster that it appears to be part of the gaster itself. The abdomen is an elongate cylinder, usually about three times as long as it is thick or wide. The genitalia may become more extruded several days after emergence or following flight. Thus, within the same species, the external genitalia may or may not be conspicuous.

MYRMECOCOLES OR ARTHROPOD ASSOCIATES OF THE ARMY ANTS

No attempt was made initially to limit this study to "inquilines" or "myrmecophiles" in a strict sense. Preconceived ideas or definitions of what is a "myrmecophile" may eliminate some arthropod from consideration even though its life cycle or behavior may have direct or indirect connections with the ants. Therefore, all arthropod associates or "myrmecocoles" were collected. However, since it was impossible to obtain identifications for many of these thousands of myrmecocoles, taxonomic work has been concentrated on those species thought to be the most closely associated with the ants. Moreover, the discussions of the groups of arthropods vary primarily in accordance with the state of taxonomic knowledge of each group.

Park (1929: 195) first used the term myrmecocoles to refer to all arthropods (other than the ants) found within an ant nest. Since other classifying terms are based primarily on the ecology or behavior of the arthropods, this noncommital term avoids the common practice of classifying an animal according to its behavior before its behavior is known. As far as possible more definite terms such as ectoparasite have been used. However, when such specific terms are not justified, I have used myrmecocole and broadened its meaning to include all animals with which the ants come in contact, including prey, predators, parasites and myrmecophiles. This usage is the same as that for myrmecoxene as used by Delamare-Deboutteville (1948: 315). However, the word myrmecoxene was proposed and used by Emery (according to Janet, 1897: 70) and also was used by Wasmann (1896: 412) to mean a symphile associated with ants.

(Symphiles are true guests which are often fed or reared by social insects, are not attacked by the host, and often have secretions upon which the host feeds.)

The myrmecocoles of army ants can be divided into the following three ecological groups according to where they are found: (1) those associated with swarm raids; (2) those found in the refuse deposits or areas where dead army ants and the remains of the booty of the ants are dropped; and (3) those found within the nests or on the ants. The species usually referred to as "myrmecophiles" are almost exclusively restricted to the last group.

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Although authors frequently claim that so many people have assisted in a project that it is impractical to list them all, I believe the generous help which has been given to me deserves more complete acknowledgment. Furthermore, a list of the specialists studying the various taxonomic groups may be of help to others working on similar projects.

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LOCATIONS OF FIELD WORK

Canal Zone Biological Area

The arthropods associated with army ants were studied at the Canal Zone Biological Area primarily from 11 February to 19 August 1956 by the author and his wife, Marian E. Rettenmeyer. Less detailed observations were made from 31 January to 7 June 1952 while I was assisting Dr. T. C. Schneirla in studies of army ant behavior. Similar work from 25 January to 31 March 1955 allowed more time to collect and study myrmecophiles, and extensive sampling of the refuse deposits was done during this period.

The Canal Zone Biological Area was selected as the site for this study for several reasons. This location can be easily reached from any part of the United States within two days. The area is ideally suited for work with army ants because of the combination of excellent permanent field laboratories adjacent to a tropical forest with an extensive system of trails. Army ant colonies are abundant, and a colony of some species can usually be found within several hours at any time of year or day. In addition, Dr. T. C. Schneirla and his associates have investigated the behavior of army ants there intermittently since 1932.

The Canal Zone Biological Area is a biological preserve comprising all of Barro Colorado Island. This island is approximately in the center of the Canal Zone between 9° 8' and 9° 11' north latitude and between 79° 49' and 79° 53' west longitude. The region became an island in 1914 when the Chagres River was dammed to form Gatun Lake as part of the Panama Canal. It has been a biological preserve since 1923 and at the present time is administered by the Smithsonian Institution. The island has an area of about six and one-half square miles or almost 4,000 acres. It is about three miles in diameter with a shore line at least 25 miles long. There are a few small clearings, but about half the area is covered by primeval forest, and the other half is second growth 40 to 100 years old. Enders (1935: 387-388, plate 1) has discussed the ages of the different areas of the forest and published a map based on the height of the trees about 1930. The forest is frequently called jungle or rain forest, but it is more accurately described as "evergreen seasonal forest," which is an intermediate formation between the true tropical rain forest and the semievergreen and deciduous seasonal forests as classified by Beard (1944, 1955). An excellent system of permanent trails extending throughout the island greatly facilitates the finding of ant columns and the subsequent tracking of the routes the ants follow. In addition, numerous streams radiate from the center of the island to the coast, and these can be used, especially in the dry season, to supplement the trails.

There is a well-defined, but not too severe dry season from about January to April when the mean rainfall is less than three inches per month. Often there is less than one-half inch of rain during each of the driest months of February and March. During this period some of the trees lose their leaves, the leaf litter becomes dry, and the clayey soil cracks. The rainfall of the rainy season months from May through December is usually ten to 20 inches per month. A graph of mean monthly rainfall for 1925 to 1939 is given by Schneirla (1949b: 12). The months of January and April are quite variable and can be considered either dry or rainy season depending upon the rainfall of the specific year. Since there were 5.57 inches of rain in January 1956, including over two inches in the last week of the month, this month should not be considered typical of the dry season. However, it was considerably drier than the previous months. During February, March, and April between 2.1 and 2.6 inches of rain fell each month, which is slightly above the average precipitation, and the relatively even distribution of the rain made the dry season of 1956 a moderate one. The dry season of 1952 was more pronounced with rainfall totals for January through April of 2.40, 0.39, 0.11, and 5.46 inches respectively. In 1955 the dry season had a more gradual beginning and lasted longer. In December 1954 only 7.25 inches of rain fell, which is rather low for that month. The months of January through April had respectively 9.05, 0.46, 0.90, and 0.37 inches.

Observations were thus made during most of the dry seasons of three years, during the transition period from dry to rainy season in two years, and during early rainy season in one year. No observations have been made during the rainy season after 19 August. (Dr. Schneirla and Dr. and Mrs. R. Z. Brown have observed the army ants during this period on Barro Colorado Island.)

Additional information on Barro Colorado Island and its ecology has been presented by Allee (1926a, 1926b), Chapman (1929, 1938), Enders (1935), Kenoyer (1929), Moynihan (1959), Standley (1933), Williams (1941), and Woodring (1958).

Vicinity of Lawrence, Kansas

In Kansas, army ants were observed without my making any attempt to follow individual colonies. Several colonies were found within the city limits of Lawrence, Kansas, or on the campus of The University of Kansas. These are residential areas having houses alternating with large lawns with scattered trees. No extensive cover by trees or shrubs exists near the sites where the ants were seen. Several other colonies were found in or near open fields, part of which were cultivated at the time. In these areas there also was little tree cover, but fewer buildings, roads, etc., that might hinder the ants' emigrations or raids for food. A few colonies were found at The University of Kansas Natural History Reservation. This is an area primarily of eastern hardwood forest with some areas of grassland. Colonies were found in both the woodland and in the open fields. General information about this reservation and the areas where the colonies were found has been published by Fitch (1952). These parts of Kansas receive a mean annual precipitation of about 35 inches. The only genus of army ants found in Kansas is *Neivamyrmex*; its range extends only about 200 miles north of Lawrence.

METHODS FOR STUDYING ARMY ANTS AND MYRMECOCOLES

Identification of Species of Army Ants

Since the behavior of the army ants varies according to the species, it is useful to be able to recognize the species of ant in the field. Often several colonies of different species may be located in one day, and one may wish to study the rarest species first or to study the species most likely to have certain myrmecophiles living with it.

The odors of the various species are different but impossible to describe adequately. The more distinctive odors, such as that of *E. mexicanum*, can be useful aids in identification, especially at night in the field or when columns are so weak that only a few intermediates can be found. If one rolls a worker between one's fingers, the ant can neither bite nor sting, and the odor is more readily apparent.

Keys and descriptions for all species and known castes of army ants have been published by Borgmeier (1955). The following key was modified from those of Borgmeier with the addition of some characters to make it more useful for field identification so that with a hand lens one can identify the species of the more common army ant workers in Panamá. The key is easiest to use if both majors and small workers can be examined in the dry state rather than in alcohol.

Key to Workers of Common Army Ants in Panamá

1. Ants found in a column or nest or location unknown .... 2.
Ants found in a swarm raid (advancing mass of ants one meter to ten meters wide)................................ 10.

2(1). Antennae thick, scape about one third as wide as long .... 3.
Antennae slender, scape less than one fourth as wide as long .... 4.

3(2). Propodeum with two broad, flat, transverse dorsal carinae .... *Nomamyrmex esenbecki* (Westwood).
Propodeum rounded posteriorly, without carinae .... *Nomamyrmex hartigi* (Westwood).

4(2). Tarsal claws without tooth; largest workers 5 to 7 mm. long; relative size of head (compared with body) same for largest and smallest workers .... *Neivamyrmex* sp. (*pilosus* is most common species).
Tarsal claws with tooth; largest workers 8 to 12 mm. long; heads of largest workers disproportionately larger than bodies, in comparison with smallest workers .... 5.

5(4). Majors with elongate, hook-like mandibles (ice-tong-shaped) usually without teeth; heads of all workers dull (except majors of *E. hamatum*) (specimens should be dry to determine if heads are dull or shiny)................................*Eciton*...... 6.
Majors with triangular, toothed mandibles; heads shiny...................................*Labidus*........ 12.

6(5). Small workers with thorax brown to reddish-black, gaster orange or much lighter...Eciton burchelli (Westwood).

Small workers with thorax yellow to brown, gaster same color as thorax or only slightly lighter................. 7.

7(6). Light brown to yellow .... 8.

Brown to reddish brown .... 9.

8(7). Hind tibial spur about four times as long as wide and about as long as width of distal end of tibia; petiole with blunt anteroventral spine or without spine; majors with shiny heads....... E. hamatum (Fabricius).

Hind tibial spur about as long as wide, much shorter than distal width of tibia; petiole with long, sharp, anteroventral spine; majors with dull heads .... E. lucanoides Emery.

9(7). Propodeal spines blunt, notch between spines shallow (more like a carina with a median indentation than pair of spines); majors 9 to 10 mm. long.E. mexicanum Roger.

Two sharp propodeal spines distinctly separated by narrow, deep, V-shaped notch; majors 11 to 13 mm. long .... 10.

10(9). Majors and larger intermediates with spine on occipital angle of head (can be felt by rubbing finger over occipital area of head).... E. vagans (Olivier).

Majors and larger intermediateswithout spine on occipital angle of head.... E. dulcius crassinode Borgmeier.

11(1). Heads not shiny; majors 10 to 12 mm. long; mandibles longer than width of head and hooked (ice-tong-shaped); small workers with thorax reddish-black, gaster orange or much lighter.. *Eciton burchelli* (Westwood).

Heads shiny; majors 8 to 10 mm. (rarely 12 mm.) long; mandibles shorter than width of head; mandibles triangular and toothed; thorax same color as gaster..... 12.

12(5, 11). Color dark brown to black or reddish-black; petiole without anteroventral spine.... *Labidus praedator* (F. Smith).

Color reddish-yellow to reddish-brown; petiole with anteroventral spine.................. *L. coecus* (Latreille).

Methods for Finding Nests or Bivouacs

Since army ant columns are normally continuous, it is theoretically possible to follow any column to the nest. If it is a raid column, one can follow it in one direction to find the advancing front, or in the opposite direction to find the nest. If the ants are emigrating, the column will lead from the old to the new bivouac. Therefore, it is useful to know first whether a column is a raid or emigration column.

Raid and emigration columns can often be distinguished on the basis of the amount and consistency of the traffic. Raid columns usually show frequent waves or spurts of traffic and at times there may be gaps of one or two meters along the route where there are no ants. The rare gaps in emigration columns seem to be caused by some direct disturbance of the column. The emigrating ants run with a more even pace, showing no hesitation, and about 90% generally are going in one direction. In addition, raid columns of the more epigaeic species, *E.*

burchelli, E. hamatum and L. praedator, are one to five ants wide as a rule, whereas the emigration columns are five to ten ants wide. The more subterranean species commonly have raid columns one to three ants wide and emigration columns two to five ants wide. If ants are running in both directions along a column, in more or less equal numbers, it is almost certain to be a raid column. However, if they are mostly going in one direction it could be either a raid or emigration route. Raid columns are not apt to have guard workers or ant roadways.

Different species of army ants start raids, and the emigrations which may follow raids, at different times of day. Since raids of Eciton hamatum and burchelli typically start about dawn, most columns of these two species until about 8:00 a.m. have ants moving primarily away from the bivouac without carrying any booty or brood. Any objects being carried by the workers at this time of the morning can be expected to be booty being carried toward the nest. The best time to find columns and nests of these two species is between 9:00 and 11:00 a.m. Then the raid columns are longer than earlier in the day, increasing their chance of being found. They also are wider with more ant traffic, including more booty carriers returning to the nest, making the columns easier to trace. Where ant columns fork, these booty carriers are of considerable importance in indicating the direction to the bivouac. If no booty carriers are present, one can deduce the direction of the nest with less certainty by the direction of most ant traffic and the angles of the fork. In most cases the angle between the two outward branches is more acute than the angles between either of these and the basal column leading to the nest. If several columns can be seen close together, the predominant traffic on all of them is most apt to be moving in a consistent direction (either all away or all toward the nest).

About 11:00 a.m. there is a decrease in traffic away from the bivouac on columns of *hamatum* and *burchelli*, and more workers both laden and unladen return to the bivouac. During the siesta period between about 11:00 a.m. and 3:00 p.m., columns of all the species of army ants, even the most epigaeic species, *E. burchelli* and *hamatum*, are difficult to follow to the bivouac. Columns are thinner or absent, and booty may be deposited in caches rather than carried back to the bivouac. Thus, booty may be seen being carried both toward and away from the bivouac.

In late afternoon and early evening there is frequently an increase in raiding activity. If most ants are carrying booty, and they are running in a consistent direction in thin columns of about three ants wide, these ants most probably are returning to the bivouac. If the column is wider with booty being carried in both directions, it probably is the start of an emigration route. Later booty will be carried away from the old bivouac in increasing amounts and more unladen workers will be running in even wider columns away from the old bivouac. By the time brood is seen in the column, the new bivouac is usually being formed. Although workers carrying booty may be scattered throughout an entire emigration, they are more concentrated at the beginning.

If an emigration is going to occur, there will be an increasing exodus of ants from the old bivouac, and a large number of these will be carrying larvae (or occasionally eggs or cocoons). Emigrations of *hamatum* usually begin between 3:00 and 6:00 p.m. and end between 6:00 and 9:00 p.m. Emigrations of *burchelli* may begin between 3:00 and 9:00 p.m. and end between 10:00 p.m. and 4:00 a.m. Rarely, they start and end later. Therefore, between 6:00 and 8:00 p.m. is an excellent time to hunt for these two epigaeic species.

Colonies of the two swarm raiders, *E. burchelli* and *L. praedator*, can sometimes be located by the noise of the flies and ant birds which accompany swarm raids (see section Raids of *Eciton burchelli*). On two occasions I have found bivouacs of *burchelli* by tracing the odor coming primarily from the refuse deposits next to the bivouacs.

Since the activity of the more subterranean species of army ants cannot be as consistently predicted by the time of day, it is more difficult to determine whether their columns are raid or emigration columns. However, the time of day is of some help in addition to the differences (given above) in the appearance of the two types of columns. The subterranean species raid primarily in the evening, at night, or in the morning before 10:00 a.m., and emigrations may follow these raids. Booty being carried in both directions along a column may indicate an emigration is beginning. Emigrations were never seen during the warmest parts of the day, and rarely in the morning. If an emigration column is seen in the morning, it probably will become weak and stop before about 10:00 a.m. unless the day is cloudy or rainy. Columns of the hypogaeic species are more often found during rainy days or in the rainy season. However, both raid and emigration columns may go underground a few to many meters from the actual bivouacs which are subterranean or in sheltered places, such as rotten logs. One can often determine whether the bivouac is near the hole into which the ants disappear by pounding or jumping on the surrounding ground. If ants pour out of the hole, the bivouac or a large cluster of ants is almost certain to be only a few centimeters below the surface. If no ants appear by this technique, it is usually futile to dig where the column disappears into the ground. One may be able to find the bivouac by investigating appropriate sites in the vicinity. These may be logs (under or inside), hollow trees, cavities under stones or large roots, spaces between buttresses of trees, brush heaps, and areas of dense vegetation such as the bases of clumps of bamboo, palms, or terrestrial bromeliads (wild pineapple).

Mounds of dirt at the edges of logs or rocks can be useful indicators of ant activity which might be due to Ecitonini. All species of army ants are capable of digging, but normally the epigaeic species do not do so. The subterranean species apparently never dig complete nests but probably always do a little digging at their bivouac sites. Species of *Eciton*, *Labidus*, *Nomamyrmex* and *Neivamyrmex* have all been observed to enlarge either their bivouac sites or the holes through which their columns enter the ground. If these ants remove a large quantity of dirt, they pile it in loose mounds which do not extend more than a few centimeters from the entrance to the bivouac.

In addition, *Labidus* and *Nomamyrmex* may make dirt passageways for raid or emigration columns. These passageways differ from those of termites in that the earth is not cemented together in any way but is simply piled up. The passageways may be open at the top or some parts of them may be completely closed to form tunnels as in figure 8. Such tunnels without ants in them during the daytime may contain ants at night. One species of army ant, *Nomamyrmex hartigi*, has been reported raiding termites inside the tunnels made by the termites on the sides of trees and on other surfaces.

Searching for columns is the easiest way to find the maximum number of colonies of army ants in a tropical forest like that on Barro Colorado Island. However, the rarest species are subterranean and are more apt to be found by cutting open rotten wood, turning over rocks, logs, etc. than by finding columns. On one occasion the cutting open of a log containing a bivouac of *E. hamatum* revealed a bivouac of *L. praedator* within the same log. No column nor swarm of the *praedator* colony was seen around the log before the bivouac site was cut apart. On another occasion a sample of army ants was unknowingly included in a sample of leaf litter put into a Berlese funnel. This small species of *Neivamyrmex* was apparently raiding on or near the surface of the soil under leaves.

Turning over stones, especially if there are piles of loose dirt around them, is the most successful way in my experience for finding colonies of army ants in temperate regions. Ecitonini in temperate regions place their larvae under stones like many nondoryline ants presumably because of the warmth retained by the stones. If these ants disappear from under a stone in the evening, the next day they may return to the same spot.

Schneirla has used string to mark the positions of bivouacs and to indicate the emigration routes. One can avoid losing an ant colony or becoming lost oneself in the tropical forest by using such trails of string. Trails of vegetation, such as palm fronds, take much more time to make and are more disturbing to the ants. Some kind of trail is necessary for one to be able to relocate the bivouacs especially at night. If one wishes to indicate the route more precisely, the string can be put only a few centimeters away from the ant trail. For more accurate indications of the route, toothpicks have been used most successfully. I have also used spots of colored paint next to the trail, but the ants were disturbed by the odor of aromatic paint solvents. Toothpicks were used to mark trails to refuse deposits by placing the toothpicks two centimeters to the right of the center of the column.

Colored or marked toothpicks were used to indicate particular places along these columns.

Measurements of Distances

The distances between bivouacs reported in this paper were estimated by using the trail markers on Barro Colorado Island as guides and by pacing off the route taken in following the colony to its new bivouac. This method apparently has been used in most cases by Schneirla. Therefore, the distances are neither the shortest distances between any two bivouacs nor the distances that the ants actually traveled. No accurate measurement has apparently been made of the distance an ant travels on an emigration. Without including possible backtracking toward the old bivouac, the more zigzag path of an individual ant could easily be two or more times the distances reported in this paper.

Dimensions of bivouacs and lengths of refuse columns are based on actual measurements.

Methods for Sampling Ant Colonies

When a colony is found for the first time, one usually wishes to know the age and sex of the brood in order to predict the emigrations and other activity of the colony. The methods used for these predictions are given below in the section entitled, Determining Ages of Broods and Position of Colony in Activity Cycle. However, the way in which a sample is taken affects not only the estimate of the brood's age but also the number of myrmecophiles in the sample.

When a colony was first found, its bivouac was usually partially knocked down with a machete, and the brood and workers sampled. Samples were usually taken by picking up clusters of ants with forceps 25 to 30 cm. long and putting these clusters directly into 70 percent alcohol. On a few occasions attempts were made to etherize bivouacs, but the ether immediately excited the ants. The bivouacs fell from their supports, and the ants dispersed through any slight openings that were not plugged tightly before the ether was applied. A much more successful method was to collect the ants as quickly as possible using a large polyethylene plastic bucket into which they could be knocked or scraped. Where it was necessary or most efficient to use one's hands for scraping up the ants, leather gloves were useful equipment. The majors can bite through them but not deeply, and the stings cannot penetrate the leather. Cloth wrapped around the wrists prevented the ants from running up open sleeves. These latter methods were used only when I attempted to collect entire colonies or when a bivouac in a difficult location had to be thoroughly torn apart. Normally samples of any size can be taken if one grasps the ants with forceps using no protection against stings. Since the brood is primarily lying on top of the workers, a large bolus of workers from the center of a bivouac will usually include much brood. A mixed cluster of workers and brood can be picked up with forceps with no noticeable injury to the larvae.

Schneirla has reported that the brood in colonies of <u>burchelli</u> and <u>hamatum</u> is placed in the bivouac in approximate order of size: the eggs or smallest larvae being in the center, the largest larvae at the periphery. This appears to be true in compact bivouacs. However, if the bivouac contains much vegetation or is of the "compound" type (Schneirla, Brown and Brown, 1954: 273, 277), the brood may show no arrangement at all and be widely scattered throughout the bivouac. For these reasons, it is advisable to sample the brood from several areas of each nest rather than from a single spot if one wishes to get the most accurate picture of the size range.

Colonies of Labidus should be more thoroughly sampled from many parts of the bivouac, because this genus is most likely to have brood of all ages within a single nest. Since there are some indications that some myrmecophiles are found most frequently with brood of a certain age, this sampling technique may yield a greater variety of myrmecophiles. Myrmecophilous insects in general are decidedly more abundant with eggs and larvae than with cocoons and adults of the ants.

The brood of subterranean army ants may be scattered throughout much dirt or wood, or it may be partially sorted by size or age. Some sorting by size was noted in a colony in a rotten log, probably because the ants could enter the smallest passageways with only the smallest brood. Thus, one should examine all size passages for some may contain only eggs or young larvae belonging to the same brood or an additional brood of the colony. Similarly the ants which may place their young under stones may have additional brood or brood of a different age deeper in the soil. Except for the more peripheral position of the larger (but not necessarily older) larvae in bivouacs of hamatum and burchelli, there does not seem to be any distinct arrangement of army ant brood according to size. However, so few subterranean bivouacs have been examined that it is impossible to state if the brood is placed in a regular position or arrangement within the bivouac. When two broods of distinctly different ages are present, such as the pupal and egg broods in a late statary colony of E. burchelli, the broods are usually completely separate. Thus, in statary colonies or colonies with a cocoon brood, one should always look for a brood of eggs.

Different ages or sizes of adult workers can be collected by several sampling techniques. The smallest workers do not seem to be common in raid columns or refuse columns. However, in the bivouac these workers are usually concentrated around the eggs, and the queen may be completely surrounded by a tight mass of over 1,000 small workers. If one tears a bivouac apart in searching for the queen, she is apt to move away from her original location in the bivouac. Most of the numerous small workers then do not stay with her, and there is a larger number of excited major workers around the queen. These dense masses of either small workers or majors are the best indicators of the location of the queen within masses of ants. Although the workers are greatly excited by their queen and attracted to her, no successful method has been devised for attracting and capturing large numbers of workers by using a queen as bait.

Each colony usually has a single queen except at the time when broods of males and queens are produced. It is possible that some species, especially the more rarely found subterranean army ants, have more than one queen; six and ten queens but no males were found in two colonies of Neivamyrmex carolinensis (Schneirla, 1961: 5).

It is sometimes desirable to collect numerous major workers since these have more myrmecophiles on them than small workers. A sample of over 90% majors can be collected easily from a bivouac of E. hamatum by brushing a pair of long (25 to 30 cm.) forceps lightly over the ants. Holding a major by the tips of the forceps also seems to help arouse the other majors which run up the forceps and bite them or cling to the other majors. A small cluster of five to ten majors is then transferred to a bottle before they have time to run to the top of the forceps. This technique does not work as well with *burchelli*, possibly because the proportion of majors is lower, and the smaller workers are more aggressive than those of *hamatum*. With other species of *Eciton*, this technique has not been adequately tried. A similar technique of lightly brushing a major worker held in forceps along raid or emigration columns sometimes attracts additional majors to the area. This has been most useful with *E. mexicanum*, *L. praedator* and *L. coecus*. However, sometimes this technique does not work, and the ants disappear completely.

Except as indicated above, I have not been able to find a method for selectively collecting workers of certain sizes. However, since the largest workers spin cocoons first, one can collect major and submajor cocoons in spinning clusters and later collect cocoons of decreasing sizes down to the minors which are the last to spin. Similarly, one can sometimes find clusters of cocoons in bivouacs on the last statary or first nomadic days. These will be the smallest workers which emerge last.

If one wishes to collect a large sample of callow workers, this is best done from the bivouac or emigration columns of the first or second nomadic days. The callows take practically no part in the raids during the first days of the nomadic phase. On the first nomadic days one can sometimes collect callows almost exclusively during the middle and latter parts of an emigration. (Additional information on collecting from emigration columns is given under the section on Collecting Queens.)

Sexual broods may be more difficult to find within bivouacs than worker broods because of the smaller number of male and queen larvae. The immature reproductives and alate males are often scattered throughout the bivouac, and the large isolated larvae and cocoons can be easily confused with booty.

By using lights to attract males, an additional method of collecting army ant workers was discovered. On several occasions subterranean colonies of Labidus and Neivamyrmex were found attacking the insects which dropped below the light boards. The ants did not run up the walls or cloths behind the lights to attack the insects resting there, but they killed many insects on the ground below the lights. Most of the raiding activity took place in grass, possibly because the lights repelled the ants in more open areas. The ants remained in these areas for at least three and sometimes as long as ten hours, whereas without the abundant source of prey, the colonies would have shifted their raiding to other sites. These ants could be most readily collected in large numbers by holding insect prey in the midst of the ants. When a tettigoniid was held at the tip of forceps, the ants would attack it on all sides, and vibrating or shaking the forceps often increased the number of ants that would bite the insect. In addition, more of the largest workers would join the attack. When the insect was largely covered with ants, it could be transferred to a bottle of alcohol. This method worked better than using an aspirator, since the latter would not both attract and keep more of the larger individuals in the vicinity.

Wheeler discovered that Labidus coecus could be attracted and trapped in great numbers by burying a few walnut or pecan kernels in the lawns near Austin, Texas (Wheeler, 1910: 264). This species will also eat roasted peanuts, but my attempts to attract coecus to these nuts on Barro Colorado Island were successful on only one of four attempts when the nutmeats were put next to raiding columns. Other species of army ants including Labidus praedator showed no attraction to dried or roasted peanuts, walnuts, pecans or almonds. In Costa Rica hundreds of workers of Labidus coecus were trapped in lard when they apparently tried to feed on it (C. W. Palmer, in letter).

Estimating the Size of Colonies and Broods

There are two main methods for estimating the size of colonies of army ants. These are based (1) upon counting a fraction of the colony or (2) measuring the time required for a counted number of ants to pass a given point on an emigration. Both methods are subject to considerable error.

Since it was impractical to preserve whole colonies, which may have a volume of over three gallons of tightly packed ants, counts were made from small samples. This method required making an estimate of the proportion of the colony which was included in the sample. Since bivouacs are seldom symmetrical and normally are highly irregular in shape with indefinite amounts of vegetation, parts of logs, etc., inside of the masses, these estimates are highly inaccurate. In addition, most samples were taken when large numbers of workers were raiding or when part of the colony had emigrated. Most of my "large" samples range from 200 to 300 ml. of loosely packed workers preserved in alcohol. Such a sample is probably about 1/50 to 1/100 of a hamatum colony. Samples were subdivided into volumes of about 100 ml. using a 250 ml. graduated cylinder with an inside diameter of 35 mm. The preserving fluid was drained from the ants and the workers packed tightly by tamping them repeatedly with a glass rod as they were placed in the graduate. All workers and immature stages were counted except for large samples of eggs or the youngest larvae which were estimated. The presence of a few thousand eggs or young larvae in the samples appears to make no appreciable difference in the counts of workers because the brood fits into the interstices among the workers. Both etherized and preserved volumetric samples contained approximately the same number of workers if the workers were sufficiently anesthetized to prevent their movement.

Since broods are normally kept within the bivouac for most of the day, the entire brood could be more readily seen than all the workers. The proportion of brood actually taken can be most easily judged when the brood is youngest, since at that time it is highly concentrated and has a small volume. The older the brood, the more dispersed the larvae and pupae usually become. In many cases, the young brood can be entirely exposed in a few seconds. When the brood is old and more dispersed, one has to tear apart the complete bivouac in order to see the entire brood. Furthermore, the ants carry away and cover up the brood almost as quickly as it can be exposed.

The rate of emigration of ants was estimated by recording the number of seconds for 50 ants to pass a given point. These counts were later reduced to 25 ants, which required less time and gave results of comparable accuracy. At half hour intervals four timed counts were made in direct succession unless the traffic was fluctuating enough that more frequent counts were necessary. The mean rates were used to determine the number of ants which emigrated throughout the entire period when the column was watched. Ant traffic toward the old bivouac also was counted and subtracted from the outward traffic. Of course the large number of ants which left the bivouac throughout the day on raid columns as well as those that emigrated before counting was started could only be estimated. This was done by judging what percentage of the colony had already reached the new bivouac compared by volume with the old bivouac at the same time. In most cases about half of the ants probably were on raid columns or at the new bivouac. This method is considered more accurate for counts of the worker population than the method based on preserved samples (unless one can collect at least one fourth of a colony). However, it still is very inaccurate. It is difficult to count the ants at their maximum speed which approximates 50 ants in seven seconds. At these speeds the ants were counted in groups of five. It is difficult to estimate the numbers of ants along the route between the bivouacs and often is impractical to make counts close to the new bivouac. In addition, one still has to estimate the volume or proportion of the ants in the two bivouacs at the time when counting is started.

Examination of Samples

Some samples of living ants were examined in Panamá, after they were anesthetized with ether, in order to find myrmecocoles for additional study. The ants were kept in a battery jar or polyethylene pail and anesthetized by adding a small rag soaked with ether. Then the ants were poured out, a few hundred at a time, on a white enamel pan and examined to remove the myrmecocoles. Unanesthetized ants were also sorted, but their activity more than doubled the time required.

Unfortunately, both these methods reduce the number of myrmecocoles which can be recovered from a given sample of ants compared with preserving the ants in alcohol directly at the nest. Although exact comparable data cannot be given, when a large quantity of ants was brought to the laboratory alive, myrmecocoles in the sample were frequently found dead. The transporting of the ants kept them constantly excited, and probably they attacked the myrmecocoles as well as their own brood under these conditions. Dead and injured Staphylinidae were found in these samples, and Thysanura and Phoridae were notably scarce or absent. When the ants are anesthetized in a container, many of the mites drop off the ants and stick to the moist sides of the container. It is difficult to wash them off, and many are undoubtedly lost. For determining the positions of mites on the ants, it is best to collect samples of 100 to 500 workers in a large container (300 ml.) and then examine each worker under a microscope individually. This technique was used with all the common species of army ants found in Panamá and Kansas. However, since this method is so time-consuming, it was not used enough to find the positions of all the common mites. Some mites stay on the bodies of the ants after they are preserved, but most mites and all the myrmecophilous insects fall off.

Determining Ages of Broods and Position of Colony in Activity Cycle

The approximate age of the larvae in a sample and the position of the colony in the nomadic phase were determined by comparing the lengths of the largest larvae with those of the largest full-grown larvae. (Larvae taken when cocoon spinning had just begun were considered full-grown.) The graph of growth rates published for <u>hamatum</u> larvae

(Schneirla and Brown, 1952: 15) can also be used, but this graph is based upon means which are more difficult to determine than the maximum lengths. Schneirla (1961: 10) has also published a graph of the growth rates including the maximum and minimum lengths of male and worker larvae of Neivamyrmex nigrescens. Since the largest full-grown larvae are the same length or about one millimeter longer than the length of the adult major workers, the relative age of larvae of other species of army ants can be estimated. The lengths of the larvae were measured to the nearest 0.2 mm. using a stage grid and a stereoscopic microscope. Following the method used by Schneirla and Brown (1952: 13), separate anterior and posterior measurements were made to include the curvature of the larvae. More accurate determination of the larval ages can be made by measuring leg buds (Tafuri, 1955). For all brood samples, measurements were made of the ten largest and the ten smallest larvae which were selected by eye from a petri dish. All samples had previously been examined and divided into separate vials of workers and larvae. When samples were small, each entire sample was examined to pick out 20 for measuring; when samples were large, larvae from different parts of each sample were put in the petri dish until the bottom of the dish was covered. Larvae must be selected from different parts of the sample, because they settle out according to size. Where eggs and larvae were found in the same sample, the eggs and not the smallest larvae were measured. Where larvae and cocoons were found in the same sample, the ten smallest larvae and the ten biggest prepupae or biggest larvae in cocoons were measured. Prepupae can be distinguished from larvae without opening the cocoons by the presence of a fecal pellet in the narrower posterior end of each cocoon. Within the cocoons prepupae can be distinguished from pupae by their shape. If only cocoons were found, the ten smallest enclosed larvae or prepupae and the ten largest pupae were measured. In addition, the pupae were divided into four age classes: (1) with short leg buds; (2) white, with legs expanded; (3) slightly pigmented; and (4) dark, *i.e.*, about the same as the color of emerged callows for the species.

Colony Designations and Marked Queens

Colonies studied by Schneirla or his associates are designated by the symbols he used. Included are all colonies which I observed in 1952 and 1955. Typical designations would be '48 B-II or '46 H-B. The numbers '48 and '46 usually refer to the year when the colony was first found. However, colony '48 B-II, for example, was studied only during 1947 and was apparently designated '48 because most of the work during that trip to Panamá was during 1948. All colonies which I have studied since April 1955 have been designated with the letter "E" and numbered in chronological order starting with E-101 regardless of species or locality. A complete list of these colonies is given in the appendix. Colonies studied by other persons or samples received from different collectors have been given colony numbers prefixed by "D" starting with D-101. Queens are referred to by their colony designations.

In order to be certain that observations over a period of time concern a single colony, two methods have been used. One is to mark the queen for subsequent recognition with slits or notches cut in the abdominal terga with iridectomy scissors (Schneirla and Brown, 1950: 274). The edges of the cuts darken, and the queen can be identified by these slits if she is found again in a few days or after several years. The usual procedure, however, has been to follow every emigration in order to avoid losing a colony. These emigrations must be followed completely, as shown by several cases in which a second colony near by with almost identical brood was accidentally mistaken for a colony which had been followed on previous days. Whether a colony is the same as another colony found one or a few days earlier, can be determined by removing the queen. After several hours some of the workers will run along the previous emigration routes and some of the earlier raiding trails. They should be found at the preceding two or three bivouacs of a colony within about a day. This technique is not recommended if a colony has a sexual brood, because the colony may not accept their queen when she is returned as reported by Schneirla and Brown (1950: 330-331). The queen should not be kept away from her colony any longer than necessary, since queens even when kept with food and several workers may die within one or two days. Furthermore, after a few days the colony may combine with a second colony of the same species. How soon this may happen is unclear because few cases have been reported. Schneirla and Rosenblatt (1961: 226) have reported that if a colony "has been without its queen for as little as 12 to 20 hours, the workers intermingle readily with those of a colony of the same species when its columns are encountered, instead of becoming disturbed and remaining apart as normally occurs. When a queen is removed from a colony of _E_. _burchelli_ or _hamatum_ with a worker brood, backtracking columns are active for 24 hours a day without appreciable interruption. These columns are most likely to follow the previous emigration route during the first few days after their queen has been taken, and thereafter the columns seem to deviate more from the previous trails. Although a similar reaction has been seen with other species, the columns may be present only for a few hours; they may be restricted to inconvenient hours between

8:00 p.m. and 7:00 a.m.; and they may not follow the exact emigration route used earlier.

Collecting Queens

Queens running in emigration columns can be easily picked up with forceps. However, sometimes the column must be watched continuously for several hours and possibly more than eight hours before the queen passes. There is always the possibility the queen emigrated before observations were started, and she may be overlooked even if the whole emigration is watched. The best observation points for finding the queen and myrmecocoles are long logs or open clear areas of rock or soil. In these places the queen is most easily seen, and there are fewer places where the queen can hide in case she is dropped or missed in the first attempt to pick her up. If there are no workers, or only a few workers riding on the queen, she can be picked up with practically no disturbance of the column. There may be a slight ripple of excited workers running in both directions from the point where the queen was taken. This excitement disappears in a few seconds, and the ants complete the emigration. Backtracking does not start until some time (probably a few hours) later. If a minimal amount of disturbance of the entire colony is desirable, taking the queen on an emigration is the best method.

The queens normally leave the old bivouacs after 50% and usually after 75% to 90% of the ants have left, although the queen of Neivamyrmex nigrescens may emigrate somewhat earlier according to Schneirla (1958: 245). One would expect that the time when a queen of any subterranean army ant colony leaves the bivouac may be more variable than the time for a queen of an epigaeic species, since the hypogaeic bivouacs are irregular in shape and the queen sometimes may be located near the side of the bivouac where the emigration column starts. The burchelli queen usually leaves the old bivouac between 8:00 p.m. and 11:00 p.m., and the hamatum queen usually leaves the old bivouac between 6:00 p.m. and 8:00 p.m. (see table 1). However, an emigration occasionally is interrupted, and she may not leave until the next morning. Other species may start emigrations in the early morning, and the queen may not emigrate if she remains too long in the old bivouac. In these cases the emigration will be completed on the following evening, and the queen may appear early in the column. For this reason, when one watches an emigration of one of the more subterranean species of army ants, one cannot be sure he is seeing the whole emigration even if a transition from raid to emigration column is observed.

While watching an emigration, one can usually tell that the queen is approaching the observation point by an increase in the excitement of the workers. More majors appear in the column, and more workers of all sizes run back towards the old bivouac. Many workers may run short distances and then turn and run in the opposite direction along the column. The column frequently becomes wider, and more "guard" workers stand along the edges.

If the queen is dropped when one attempts to pick her out of the column, or if she is stopped by an obstruction or break in the emigration column, a section of the column may continue to be excited for over an hour. The workers may climb on top of the queen forming a pile of workers over five centimeters high. It is impossible to predict when the queen might pull out of such a cluster and continue along the emigration route. After she proceeds along the route, the excited workers may stay in the cluster and along the column near it for at least half an hour. The behavior of these workers may cause an observer to conclude incorrectly that the queen is still within the cluster.

For the above reasons, when one wishes to collect myrmecophiles continuously in the column and also take the queen, it is advisable to try to find a stretch of emigration route which is exposed for at least five meters. One can start collecting at the end of such a section away from the old bivouac. As ants and inquilines are collected, the column invariably becomes disturbed to some extent. Then the observation and collecting point can be slowly moved toward the old bivouac. The ants which are disturbed apparently deposit some chemical which excites other ants as they reach the section of the trail where the disturbance took place. If the queen comes to such an area, either the chemical itself or the workers excited by the chemical may cause her to stop. Collecting from an emigration column near the old bivouac may prolong the emigration time for the entire colony by keeping the ants more excited and causing more of them to return to the old bivouac.

When collecting at one point along an emigration route, one should check at frequent intervals to see whether the ants have started a bypass or alternate route. It is possible that this type of alternate emigration route may occur among the more subterranean species with one route completely underground.

The queen and some myrmecocoles are more sensitive to disturbances of any kind than the workers. Therefore, lights should be dim and not directed on the queen or myrmecocoles any more than is necessary. It is better to shine a light on the column from an angle so that it strikes the ants somewhat posteriorly rather than head-on. No accurate measurements of the intensity of lights used were made. However, standard flashlights with two cells were too strong when the batteries were fresh.

About one third to one half this intensity worked better. When fresh batteries were used, putting a piece of medium to dark red glass or plastic over the light gave a light which seemed to disturb the ants less. The most useful type of light has a separate battery pack connected by wires to the light which can be worn on one's head. The light is easily directed and both hands are free for other purposes.

Collecting Males

Males collected in emigration columns almost invariably have workers riding or clinging to them. These workers should be pulled off the males before the males are put into alcohol in order to make it possible to determine the numbers and kinds of myrmecophiles riding on the males. Ideally, each male should be put in a separate vial and examined alive to determine the exact position of the myrmecophiles. Since this is often impractical, the easiest technique to use in the field is to isolate the males from brood and workers.

The males of most species of army ants have been taken only at lights. At some times of the year in certain localities, it may be possible to collect over a hundred males of a single species on one or a few nights. However, a flight of this type may not be observed again in the same locality for a year or several years. Since it is impossible to predict exactly when a large flight will occur, it is best to run lights nightly. Most flights of army ants in Central America take place during the dry season and early rainy season. In the United States they may occur from early April to November. There is inconclusive evidence that some males fly to lights only between midnight and 6:00 a.m. which may indicate that these species emigrate at this time. All male army ants are slow fliers with no ability to maneuver to escape predators or an insect net. Since they also are incapable of stinging and have a completely ineffectual bite, they can be readily picked off windows or light boards.

Males taken at lights should also be examined alive with a microscope or put individually in vials of 70% alcohol. Several species of myrmecophilous mites are known to ride on the males during flight. These and perhaps other species of mites or myrmecophilous insects may fall off the males in alcohol or if the males are put in dry killing bottles. If it is not practical to put each male in a separate vial, they should be separated into vials according to species. In most cases the males seen at light can be readily separated into species by the shape and color of the head, mandibles and abdomen.

During 1952 and 1955 between one and four 50 to 100 watt incandescent light bulbs outside the old laboratory building on Barro Colorado Island were checked almost nightly for males. The windows of the Chapman House were also frequently checked, and occasionally a "Coleman" gasoline lantern was used in the forest or at the new laboratory building for attracting insects. During 1956 a greater effort was made to check the lights several times each night. On almost every night lights were used outside the north, south and west walls of the old laboratory and the west wall of the new laboratory. At each locality an incandescent bulb of 100 to 150 watts was placed in front of a white wall or cloth. Reflector flood bulbs of 150 watts directed toward the forest with a 100 watt bulb near the white background provided the best combination for attracting the maximum number of insects. Army ant males occurred in such irregular numbers that it was impossible to determine which combination of lights might be most effective. However, there was no indication that a stronger light repelled the army ants. Ultraviolet lights also attract male army ants, and probably these lights would have given better results. On a number of nights, as many as seven army ant males were taken at the light at the new laboratory, when they were not taken at the old laboratory. On other nights, one or two males were taken at the south side of the old laboratory, but none at the west or north sides. Other males were taken when they were attracted to a "Coleman" kerosene lantern or to a headlight in the forest. Thus, a number of lights is strongly recommended for collecting males even if the lights cannot be distributed over a wide area. The finding of several colonies of subterranean species of army ants raiding the insects below the light boards was an unexpected result of the use of these lights.

Collecting Myrmecocoles

Myrmecocoles were usually collected by aspirating them from clusters, refuse deposits or ant columns. Sometimes they were found by sorting through large samples of living or dead ants. The general suggestions which were given above for collecting workers and queens along emigration columns also apply to collecting myrmecocoles. Any disturbance of the column makes it much more difficult to collect myrmecocoles. Myrmecophilous beetles and Thysanura coming to a disturbed section become highly excited. They run faster and in a devious route and hide frequently under leaves or other objects along the emigration trail or a few centimeters away from it.

Forceps should never be used for picking up any of the myrmecocoles with the possible exception of species with hard, rigid bodies, such as histerids and millipedes. All others not only are usually killed or severely injured by attempts at picking them up with forceps, but also they are frequently damaged so badly that they cannot be determined. The simple aspirator described by Borgmeier (1958: 290) seems to be the most efficient for collecting even highly fragile insects like phorids and Thysanura. The modification that I have found useful consists of a straight glass tube about 8 mm. in diameter and 75 mm. long. One end is covered with a piece of fine nylon gauze, and this end is inserted into a piece of rubber tubing about two feet long which holds the gauze in place. The gauze should be large enough that it can be shifted to a clean area when the spot over the tubing gets covered with dirt. An aspirator of this size works well for all myrmecophiles and all but the largest workers. The largest major workers can be picked up with this size aspirator, but more suction must be used, and they may become wedged in the tubing. Therefore, forceps are more suitable for the largest majors. It is important to be able to quickly take the aspirator apart to remove insects which sometimes cling to the gauze by their legs or mandibles. Most specimens will drop out of the tube unless constant weak suction is used or a finger put over the end. Thus, they can be readily transferred to vials or laboratory nests. Aspirators also were useful for collecting flies and other arthropods in and around refuse deposits and over swarm raids. The arthropods in the refuse deposits were sampled primarily by using Berlese funnels. More details on how these samples were collected and examined will be given below in the section entitled, Refuse Deposits of Army Ants and the Arthropods Found in Them.

Straight glass tubes the same size as the one used for the aspirator make excellent containers for living myrmecocoles. A number of these tubes can be placed upright in a dish of plaster of Paris in order to fill one end with a plug of plaster about two centimeters long. When the plaster has started to set, the tubes are removed from the dish, and the excess is wiped off the outside of the tubes. Before using, the tubes are placed in water to saturate the plaster, and then the opposite end is plugged with cotton. In these vials the humidity is close to 100%, which is desirable for all species of myrmecocoles and army ants.

Myrmecophilous Histeridae and Staphylinidae have been taken by others at lights, but I have never been successful at finding any at lights in Panamá or Kansas.

When watching living ants in order to collect myrmecophiles, one can easily see most of the largest insects riding on the ants. As an aid for recognizing the smaller arthropods, a list of the places where these arthropods have been seen riding is given here. The families or groups which are found on the respective parts of the ants are given in parentheses. All the insects and the larger mites on ants running in emigration columns can be seen even at night using dim red light. The smallest mites can be seen only with some magnification. Although some of these myrmecophiles have also been found in comparable positions on males or queens, the following positions refer to workers unless another caste is stated: (1) riding or being carried under heads (Histeridae); (2) under petioles or gasters (Histeridae); (3) dorsal or dorsolateral parts of heads, often giving heads an asymmetrical appearance (Histeridae, circocyllibanid mites); (4) middorsal regions of alitrunk and gaster (mites, Histeridae, Staphylinidae and Limulodidae); (5) mandibles of major workers, appearing like a large lump (Circocyllibanidae); (6) tarsi of larger workers, appearing swollen or to have dirt stuck to them (macrochelid mites, Limulodidae); (7) undersides of tibiae, appearing to have a lobe or swelling (planodiscid mites); (8) antennae, especially the scape, appearing to have a lobe or swelling (uropodine mites); (9) any part of body of adults, larvae, or booty appearing as small light or dark spots or lumps (Limulodidae, mites); (10) under heads next to bases of mandibles (neoparasitid mites); (11) under front coxae (scutacarid and pyemotid mites); (12) venter between coxae (Scutacaridae and Pyemotidae); and (13) external genitalia of males (laelaptid mites). Many myrmecophilous insects, including some as small as about one millimeter long, run in the ant column. No mites were seen to run in the ant columns during this study.

Laboratory Nests

Large samples of living ants were usually collected in three-gallon polyethylene pails and then transferred to laboratory nests. By attaching a tube to a hole cut in the plastic pail and then turning on a 50-watt incandescent light close to the pail, the ants would gradually run through the tube into another container. "Tygon" (modified vinyl plastic) tubing, formulation S22-1, with an outside diameter of one-half inch and a 1/16 inch wall was used. This tubing is translucent allowing one to see the position and size of the ants. "Tygon" formulation B44-3 probably would be superior, because it is more transparent. The combination of heat and light would usually drive the ants out of a pail in four to 24 hours. A supply of water (and booty if available) was put in a dark receiving nest. Three general types of laboratory nests were used; all are modifications of those used by Schneirla.

A vertical nest shown in figure 2 was used to keep large groups of over 20,000 workers. The main vertical sides of this nest were two sheets of glass about 26 by 40 cm. held against a wood frame. The two sheets of glass were about 25 mm. apart and rested on a foam rubber gasket cemented to the wood frame. The glass was held tightly against the gasket along each edge by wooden blocks fastened by bolts and wing nuts. These removable blocks allowed the glass to be slid off the nest from any side, or the nest could be turned horizontally, and the glass lifted vertically. Approximately half the area of the top, bottom and edges was made of wood, and the remaining area was brass screening with 78 meshes per 25 mm. Several strands of rope extended from a water bottle through a hole in the top of the nest to supply water to the ants. No food was placed directly in the nest. The ants were fed by placing food in other horizontal nests and connecting these to the vertical nest by the "Tygon" tubing.

This vertical nest worked well for holding large numbers of ants and was useful for observing the formation of strings or ropes of ants building up to a large cluster like their bivouacs. However, this nest was practically useless for observations on myrmecophiles. When myrmecophilous mites or insects were seen in the nest, they usually became lost immediately as they ran among the ants. Observations on the feeding of ants and myrmecophiles were made in horizontal nests or chambers ranging in size from about 35 by 45 cm. down to small cells about five by ten millimeters. The largest horizontal nests were wood frames with sponge rubber along the edges. A piece of glass rested on the rubber strip as in the vertical nest, but only the weight of the glass held it in place. Since the ants had some difficulty running on glass, the bottom pane of glass was covered with a sheet of paper. The largest nests were used in attempts to get observations on the ants raiding and killing insects in the laboratory, as well as observations on the flies accompanying the ant raids. These nests were also useful for observing circular columns as shown in figure 1. Columns of this kind were used to observe how myrmecophiles emigrate, since these columns reproduce many of the essential features of the ant emigrations.

Some smaller nests, varying from 15 by 15 cm. to 25 by 30 cm., were made with pieces of cloth for the bottom instead of glass. The cloth was stretched tightly and held to the wood by U-shaped wire staples from an ordinary paper stapler. When cloth was stretched tightly, the ants could not readily bite it or pull holes in it. Each nest was placed over a board so that half of its area overlapped the board. On the board was a second cloth with one end in a dish of water. Water would soak through the lower cloth and keep the one attached to the nest moist and the humidity high in the nest. Air could pass through the half of the nest not touching the board with the wet cloth. A small piece of wood under the edge away from the board kept the nest from tipping.

For most observations on the behavior of any of the arthropods, petri dishes were found to be convenient. These had a small enough area that the entire dish could be placed on the stage of a microscope. They also lack corners in which many of the guests could hide. Filter paper in the bottom was kept moist in order to keep the humidity high and to hold the paper tightly against the bottom of the dish. Blotting paper and other colored paper was sometimes used to get better colored backgrounds for photographs when white was objectionable.

Since almost all the myrmecophilous insects move rapidly, it was usually impossible to observe them alive under a microscope. To alleviate this problem, small cells were molded or cut in plaster of Paris or paraffin blocks. These cells varied from 24 by 36 mm. down to five by ten millimeters in size. Microscope slides were used as covers for these cells. Glass tubing the same diameter as the aspirator was used for an entrance to these cells. A myrmecophile could be introduced into the tube using the aspirator, and a glass rod pushed down the tube would force the specimen into the cell. Although these cells were convenient for observing myrmecophiles with a microscope or for taking photographs, the arthropods usually would not feed or carry on other normal activities in the cells.

A passageway which had both a top and one vertical side of glass was most practical for observing and photographing columns of ants and myrmecophiles laterally. This passageway was about 30 cm. long, 1.5 cm. wide and 2.0 cm. high. The base, ends and second vertical side were of wood with holes in opposite ends for connecting tubing to ant nests.

All laboratory nests and containers used for observations and rearing attempts were kept in laboratories with no temperature control (Chapman House or the new large laboratory building). The temperature fluctuated between 25° and 31°C and was usually several degrees higher than forest floor temperatures or soil temperatures where these arthropods live. Weber (1959: 154) reported a range of 25.7° to 27.8°C for temperatures of shaded soil from the surface to a depth of 30 cm. Moist filter paper, cloth or cotton in or on all nests and dishes usually kept the relative humidity high. The petri dishes and small chambers or vials used were too small for humidity measurements with the equipment available.

Photographs

All photographs were made with a Kine Exacta VX with 50 mm. Zeiss Tessar f. 3.5, 58 mm. Meyer Optik Primoplan f. 1.9, or 135 mm. Zeiss Triotar f. 4 lenses. A few were taken with the latter lens on a Praktica camera. Extension tubes and bellows were used for various extensions up to about 400 mm. A stereoscopic microscope was used only for figures 19 and 20. The films used were Panotomic-X, Plus X or Daylight Kodachrome. Copies of the colored slides were made on Panatomic-X sheet film using an enlarger. A few pictures were made with Daylight Ektachrome. Plus-X and Daylight Kodachrome have given the best results. Every picture used for the figures was made with an electronic flash having a flash duration of about 1/1,000 second. A flash with a shorter flash duration would be preferable because the ants and myrmecocoles moved so quickly that some blurring occurred. Moreover, the flash frequently caused the workers, queens and myrmecocoles to turn and run away, whereas one with a shorter flash duration might be expected to have less effect.

The Exacta was also found to be extremely useful for observing the ants both in the laboratory and in the field. A penta prism viewfinder was used with the normal ground glass replaced with a clear glass. Then the camera could be used as a wide field microscope with a great range of magnification and an exceptionally bright image. The camera mounted on an elevator tripod was much more adaptable than a microscope for viewing at any angle and rapidly switching from horizontal to vertical viewing.

II. THE ARMY ANTS

OUTLINE OF THE TAXONOMY OF THE ARMY ANTS

The ants or Formicidae are usually divided into six to nine subfamilies; one of these, the Dorylinae, includes all the ants commonly referred to as army ants. Although a few other ants have some of the habits of the Dorylinae, none so far as is known possesses all the behavioral characteristics of this subfamily (see Introduction). Wilson (1958) discusses similar habits among ants in other subfamilies.

The Dorylinae are primarily found in tropical areas of the world, and most species are restricted to areas of humid tropical forests. For many years the subfamily has been considered composed of two distinct groups: the Old and New World species. The latest revision by Borgmeier (1955) divides each of these two groups into two tribes: the Dorylini and Aenictini of the Eastern Hemisphere and the Cheliomyrmicini and Ecitonini of the Western Hemisphere. Information on the biology of the dorylines of the Eastern Hemisphere is limited primarily to Dorylus (Anomma) [see Wheeler (1910), Raignier and Van Boven (1955), Raignier (1959), and Schneirla (1957b)]

Of the two Neotropical tribes of army ants, the Cheliomyrmicini is rarely seen and almost nothing is known about the habits of its species. Only a single genus, Cheliomyrmex, with five species, is included in the tribe (Borgmeier, 1955: 58-76).

The Ecitonini includes 135 species distributed among four genera as follows: Eciton (12 species), Labidus (8), Nomamyrmex (2), and Neivamyrmex (114). About half of these species are known only from the male caste. In some cases the males and workers must have been described under separate names, but at present it is impossible to decide which species are synonyms because the castes have not yet been found together in the same colony. There are approximately 25 more species of males described than workers, indicating that subterranean workers of at least this many species remain to be discovered. Ways to recognize the Ecitonini in the field are given above under methods, along with a key to the more common Panamanian species. Complete keys and descriptions of all species of Neotropical dorylines are given by Borgmeier (1955).

Based on the morphology of the ants, Borgmeier (1955: 137) considered *Labidus* to be the most primitive ecitonine and *Nomamyrmex* intermediate between *Labidus* and *Eciton*. However, after the first queen of *Nomamyrmex* was found, he thought *Nomamyrmex* might be more primitive than *Labidus* or *Eciton* (Borgmeier, 1958a: 201). *Neivamyrmex* was considered to be closer to *Labidus* than to the other genera. The morphological evidence seems to link *Nomamyrmex* and *Labidus* more closely together than any other genera. It seems clear that *Eciton* is the most highly specialized of the four genera.

Borgmeier (1955: 173) has divided the species of *Eciton* into several groups based on morphological comparisons of all castes. The first of these groups includes *E. burchelli* (Westwood), *quadriglume* (Haliday), and *dulcius* Forel. *E. dulcius* is apparently not considered to be as close to *vagans* (Olivier) as it is to *quadriglume*. *E. vagans*, however, is also considered close to *quadriglume* (*t. c.*, p. 232). On the basis of the workers, *dulcius* and *vagans* appear to me to be one of the most closely related pairs of species. *E. hamatum* (Fabricius) and *drepanophorum* F. Smith are placed in a second species group. These two species are surely closely related, but *hamatum* and *burchelli* are also closely related based on the workers. *E. vagans* and *mexicanum* Roger are placed in a third group. This seems reasonable; however, I think *dulcius* may be more closely related to *vagans* than to *mexicanum*. Borgmeier (1955: 173) places *lucanoides* Emery in a separate group presumably mainly because of the thickened tarsi of the queen and a tooth on each mandible of the major workers. This latter character may not be of such great importance, since Borgmeier (1955: 263) states that a weaker tooth is found sometimes in *vagans* and *quadriglume*. In addition, I have found a small percentage of *hamatum* majors with distinct teeth on their mandibles. Apparently all majors of *lucanoides* have these teeth, although only three specimens of *lucanoides s. str.*, and an unstated number of *E. l. conquistador* Weber were examined by Borgmeier (1955: 263, 265). On the basis of the workers and queens, *lucanoides* may be quite closely related to *hamatum*. The differences in the petiolar spine of the workers as given by Borgmeier (1955: pl. 12, figs. 1, 6) are not reliable for all specimens. Unfortunately, the male of *lucanoides* is unknown. However, the queens of *hamatum* and *lucanoides* are also among the most similar *Eciton* queens, judging from Borgmeier (1955, 1958a).

Of the eight species of *Labidus*, four are known only from the males. Two, *spininodis* (Emery) and *mars* (Forel), are extremely rare, and no myrmecophiles have been reported from them. The remaining two species, *praedator* (F. Smith) and *coecus* (Latreille), are among the most common species of Ecitonini and have the largest geographical ranges. *L. coecus* ranges from Louisiana, Oklahoma and Texas to northern Argentina, whereas *praedator* is restricted to more humid areas. *L. praedator* and *coecus* are considered closely related among the species in the genus (Borgmeier, 1955: 83).

The genus *Nomamyrmex* includes only two species, *esenbecki* (Westwood) and *hartigi* (Westwood). The former ranges from Texas to Argentina. *Noma*.

hartigi is rarer than *esenbecki*, and although both species are known from Panamá, only *esenbecki* has been found on Barro Colorado Island.

Neivamyrmex includes 114 species of which 58 are known only from males and 36 only from workers. Borgmeier (1955: 286-289) has arranged all the species into groups, but only the species considered in this paper will be mentioned. *Neiv. legionis* (F. Smith, *pseudops* (Forel) and *gibbatus* Borgmeier are in group II. *Neiv. pilosus* (F. Smith), *postcarinatus* Borgmeier and *humilis* (Borgmeier) are in group III. *Neiv. sumichrasti* (Norton), *nigrescens* (Cresson), *opacithorax* (Emery) and *harrisi* (Haldeman) are in group IV. Among these species, *opacithorax* and *nigrescens* are considered closely related. The range of *nigrescens* is apparently included within that of *opacithorax*.

Borgmeier has divided some species of army ants into subspecies or races on the basis of morphology and color. A number of these subspecies are based on collections from one or only a few colonies. Moreover, some of the characters used to separate these subspecies are of doubtful value, and some of the subspecies appear to be sympatric. In spite of these shortcomings, these subspecies in most cases are useful categories for discussion of the geographical distribution of the ants and myrmecocoles.

BIOLOGY AND BEHAVIOR OF ARMY ANTS

Eciton hamatum (Fabricius)

E. hamatum (Fabricius) can be considered one of the more specialized, and thus, less typical species of Ecitonini. However, since it is also the species which has been most studied, it is convenient to discuss it first. It has been studied extensively primarily because: (1) it is common on Barro Colorado Island (and many other areas of humid lowland tropical forest); (2) its nests are usually epigaeic, that is, above the surface of the ground rather than subterranean; and (3) its much milder sting and smaller colonies make it easier to work with than E. burchelli, the second common epigaeic species. It should be emphasized that the term epigaeic as used in this paper is a relative one. The species of army ants can be arranged in a sequence from the most epigaeic species to the most subterranean or hypogaeic species. The more epigaeic ones nest, raid and emigrate on or above the surface of the ground. In addition, their columns are more frequently found during the day, including days during the dry season and sunny days. The terms subterranean and hypogaeic will be used as synonyms in contrast to epigaeic. Schneirla (1958, etc.) has often followed this usage of the terms epigaeic, hypogaeic and subterranean, but he has also used terrestrial in contrast to subterranean. Terrestrial should be preferably restricted to its more common usage as a term in contrast to arborial, aerial or aquatic.

Raids of Eciton hamatum

E. hamatum feeds primarily on immature stages of wasps and non-doryline ants and captures adult insects only when its raids are largest and the foragers most excitable (Schneirla, 1956b: 394). Although many species of nondoryline ants are captured by *hamatum*, it does not prey on *Paraponera clavata* (Fabricius), the largest ponerine on Barro Colorado Island. It also seems to overlook many of the smallest species of ants, and I have seen *hamatum* columns sharing the trails of *Atta* while the leafcutter ants had an active column. The two species occasionally bumped into one another, but no fighting was seen. If a raid column of one colony of army ants comes in contact with a raid column or swarm of another colony, some inconclusive fighting occurs. "Picket lines" or rows of workers of both species (or colonies) facing each other are formed along the line of contact. These workers will attack if a member of the other colony tries to cross the line, but generally there is little conflict. The ants continue their raiding by diverging away from the area of contact or one colony may cross the other along a log or liana.

The wasps that *hamatum* attacks primarily are the social Polybiinae and Polistinae (Vespidae). Even though colonies of stingless bees are common on Barro Colorado Island, I never saw any species of army ant attack these colonies and never found Meliponinae among the booty. Schneirla (1933: 269) reported that *hamatum* kills stingless bees, but such attacks must be rare. Perhaps these bees escape because their nests or the entrances to them are made of waxes, plant sap or mud which the ants cannot penetrate. Although on a few occasions I have seen *hamatum* raiding columns within one-half meter of stingless bee nests, the ants ignored these nests completely. However, adjacent wasp nests were found and plundered. Perhaps the ants are aided in finding prey by odors of the wasps, by previous chemical trails of raiding army ants, or by chemicals deposited near the nest by the wasps. A colony of polybiine wasps nesting in the Haskins Library building at the Canal Zone Biological Area had its entrance through a small hole in the concrete wall about two meters above the ground. A raiding column of *hamatum* proceeded so directly to this hole and carried off the wasp brood that it appeared they were guided in some manner over the seemingly homogeneous surface of the wall.

E. hamatum and *burchelli* will run over nests of muddaubers (Sphecinae and Trypoxyloninae) without hesitating or attacking the closed mud nests. The ants were never seen on such nests when cells were open. When *hamatum* was seen attacking nests of polybiine wasps or *Polistes*, the ants pulled off the caps of cells containing pupae and completely stripped the nest of all brood. The adult wasps were killed if they stayed on the nest. Most of them retreated to adjacent vegetation where wasps returning from foraging joined them. Excellent photographs of army ants attacking nests of *Polistes* have been published by Michener and Michener (1951, fig. 89) and Klots and Klots (1959: 248). One colony of ants (E-233) made a bivouac in a hollow log that must have been the site of a polybiine nest. After the bivouac was located, many wasps were seen flying directly to the small entrance hole in the side of the log. They all stopped abruptly at the entrance, and then most of them joined clusters of wasps on neighboring vegetation. A similar case was observed when colony '52 H-I made a bivouac in a hollow tree displacing a polybiine colony. In all cases where army ants have been observed to raid nests of vespid wasps, the wasps abandoned their nests. Since this appears to be a fairly frequent occurrence, many reputed cases of vespids starting colonies by swarming may be attributable to army ant raids.

The raids of *hamatum* have been termed "column raids" by Schneirla (1933) to distinguish them from swarm raids. These two types of raids are diagrammed in figures 69 and 70. While in swarm raids the advancing group of ants is a large mass or swarm, column raids have small groups of workers in narrow columns at the advancing edge or raid front. The individual workers comprising the advancing front are constantly changing. These advancing ants may fan out at the tips of the distal raid columns, but these groups are small and usually cover no more than one or two square decimeters of surface. Since the workers do not cover a large area at one time like the swarm raiders, *hamatum* does not continually drive out large numbers of arthropods in front of its raids. As a consequence the flies and ant birds dependent upon these arthropods are absent or rarely seen. Although I have never seen ant birds near this army ant, Schneirla (1933: 268) has reported seeing them near "unusually vigorous *E. hamatum* raids."

The raiding workers of *E. hamatum* run primarily on the ground and on the surfaces of leaves. They also climb vegetation and buildings, but rarely go more than two meters above the ground. The workers will also go into subterranean nests and attack ants living in them. During the dry season they are more apt to run under leaves and other objects rather than on top of them as in the rainy season (Schneirla, 1947: 11). However, even in the dry season they make frequent use of logs, lianas and other similar objects to cross streams and ravines and to make their raid and emigration routes shorter and smoother.

A continuous column of ants connects the advancing distal raid columns with the bivouac. When a strong raid is in progress, the base column may be one to six ants wide for more than 100 meters from the bivouac. During the hours from 11:00 a.m. to 3:00 p.m., called the "siesta period" by Schneirla, there is a decrease in raiding activity. This decrease may be more noticeable during the dry season, and Schneirla and Brown (1950: 296) have reported that the base column may even become discontinuous during the midday hours. Although at times these columns may become so weak that only a single ant can be found every one to three meters along the trail, I have never seen a raid during the dry season that did not continue to have some traffic between the bivouac and the front of the raid.

Raids of hamatum usually start shortly after dawn and are presumably initiated by the increase in light intensity at the bivouac. Any colony which does not start a raid in the early morning may start one at any time of day except during the siesta period. Temperature effects have been considered subordinate to light (Schneirla, 1938: 82); however, "regular diurnal temperature variations are mainly responsible for the existence of two 'peaks' in raiding activity, one in the later part of the morning, and one in mid-afternoon." Apparently a colony will start a raid between 11:00 a.m. and 3:00 p.m. only if it is greatly disturbed, as for instance, when a large part of the bivouac is knocked down. Although it would seem that sunlight striking a bivouac might have this same effect, no records of this are known to me. All army ants are considered blind from the standpoint of seeing an image, but they do react to different intensities of light. Army ants apparently find their way back to their nests not by any visual orientation but solely by a chemical trail. When raiding, the leading ants deposit a chemical trail which is followed and added to by the subsequent workers. The trail is probably not polarized, since the ants apparently cannot tell the direction to the bivouac solely from the chemical on a short length of trail. If a stick which is part of the trail is reversed, the ants show some hesitation only where the continuity of the trail is broken at the ends, and they do not reverse their direction (Schneirla, 1933; 1944a: 5). *E. hamatum* workers can also follow the trails of *burchelli* (Schneirla, 1944a: 3) and possibly those of any species of army ants. How long these trails last and how often they are re-used is debatable. The most outstanding cases where chemical trails appear to have been re-used involve emigration trails (see below under emigrations). On several occasions I carefully marked exact routes of raids near the laboratory on Barro Colorado Island, and subsequent raiding ants of the same species paid no attention to these when running over the same area. However, considering the number of ants following a single trail, one would expect the chemical trails of raids to be much weaker than emigration trails.

The raids appear to be largest when colonies have a "late nomadic brood", *i.e.*, a brood of larvae which is almost ready to spin cocoons. At this time a raid may consist of two or three base columns radiating from 150 to 300 meters from the bivouac. The raids are more likely to be smaller during the early nomadic phase, and on some days in the statary phase no raids may occur. On days when there are raids in the statary phase, the traffic along the columns is one-fourth to one-half as great as on nomadic raids (Schneirla, 1957a: 109).

Although raids during the nomadic phase are larger than those in the statary phase, both in the number of base columns and in the number of ants which take part, the maximal distance from the bivouac may be greater in statary raids. Since the colony is in one location for about three weeks, it can establish chemical trails for several hundred meters from the bivouac and also plunder most of the colonies of potential food near the bivouac (Schneirla, 1944c: 173). No adequate quantitative data on raid distances have been published, however.

Compared with the behavior of hamatum in the rainy season, in the dry season raid columns are more frequently under leaves, statary colonies are less likely to have raids, and nomadic colonies have smaller raids (Schneirla, 1947: 11; 1949b: 74, 78). Although these contrasts appear valid, colony '46 H-B studied by Schneirla did not show an increase in raiding in a statary period during the rainy season (May to June) compared with the two preceding statary periods during the dry season (February to April). The number of raids compared with days when the colony was observed during the three statary periods are respectively: 9 out of 19, 11 out of 19, and 6 out of 13 (Schneirla, 1949b: 20-22, 74).

Emigrations of Eciton hamatum

Emigrations start after the siesta period with an increase in traffic moving outward along one or more raid columns. Schneirla (1938: 70) has stated that the ants emigrate along the route on which most booty has been brought to the bivouac, but he has given no quantitative evidence. This outward flow may start between 2:00 and 3:00 p.m. when sunlight is still quite strong, or it may not start until after 6:00 p.m. after the light intensity has dropped considerably. Although the siesta period lull in raiding is "perhaps attributable to a combination of radiation, heat, and desiccation" (Schneirla 1956b: 400), an increase in raiding activity gradually shifting into an emigration may occur in the afternoon while these "detrimental" factors are still present and may even be more intense compared to 11:00 a.m. when the siesta period starts. No adequate data have been published to show any correlation between the activity of army ants and the atmospheric conditions during the siesta period. Perhaps some inherent "clock mechanism" is important for initiating these changes in raiding activity and the shift to emigration. Schneirla (1944b: 453, footnotes) acknowledges the lack of direct evidence for any correlation between environmental factors and the siesta period or emigration. In addition, he considers that it is "somewhat doubtful" that a "temporal memory" or similar phenomenon produces the increase in activity in the afternoon. Ants which he kept in the laboratory under ruby glass did not exhibit any noticeable increase in activity in the afternoon at the time when colonies in the forest became more active. It was not stated whether ants kept in the laboratory without covers of ruby glass showed any change in activity. In my experience they did not; however, this may not be an adequate test of the hypothesis of a possible internal clock.

Two emigrations were seen during 1956 that were finished before 7:00 p.m. One of these occurred on 8 March 1956 when colony E-127 had completely abandoned the old bivouac site except for a strand with a width of about five ants at 6:00 p.m. The queen had left the old bivouac, and the few hundred remaining workers must have left the bivouac site by 6:15 p.m. at the latest. The second case was on 11 April 1956 when colony E-141 had a strong emigration in progress when it was visited at 3:45 p.m. Some brood was being carried at that time, and at 4:00 p.m. large amounts of brood were being carried. The queen left the old bivouac at about 6:30 p.m., and the last ants left the site at

6:50 p.m. Neither of these bivouacs had been disturbed by me during the days of these early emigrations. Normal emigrations of hamatum probably never occur much earlier than in the above cases. Schneirla (1949b: 19) reports similar times for only two out of 49 emigrations for colony '46 H-B. Probably the size of a colony, and other factors within a colony influence the beginnings of emigrations. The presence of a larval sexual brood may delay the start of an emigration and prolong it. Colony E-105 with a sexual brood started an emigration on about the third nomadic day between 8:48 and 10:00 p.m. There is no data to show that some colonies regularly emigrate earlier than others.

In eight of 14 cases shown in table 1, when the queen was seen on an emigration, she had apparently left the old bivouac between 6:30 and 8:30 p.m. By the time the queen is seen on the emigration column, 75% to over 90% of the colony has left the old bivouac judging from those cases where the old bivouac has been seen at approximately the same time as the queen.

Although low light intensity may be an important factor for the completion of an emigration, it apparently is not the primary triggering stimulus. Schneirla (1944c: 159) has reported that the queen is more sensitive to light than the workers. Moreover, she will turn away from a beam of light directed on her, whereas the workers "seem virtually incapable of specific orienting responses to light." This photonegative reaction of the queen is probably important for keeping the queen in the central parts of the bivouac (Schneirla 1944c: 158-160), but may also contribute directly to her late appearance along emigration columns. All the ants have usually emigrated from the old bivouac by 8:00 to 11:00 p.m. However, if the emigration is delayed by heavy rains, as may be the case in the rainy season, emigrations may not be completed until after dawn the next morning. Schneirla (1944c: 160) reports two cases where queens were seen on emigrations during daylight. (These two cases must be less than 0.5% of the emigrations for which records exist but no accurate count is available.)

Emigrations with worker broods rarely show any signs of "ant roadways" or "flanges" (similar to figures 5 to 7) such as are common with sexual broods. (See section on Sexual Broods and Colony Divisions.) These "roadways" are composed of workers which cling to leaves or to any other objects along the path of the emigration and remain immobile while the other workers emigrate across their bodies (see figure 5). They serve a useful function, especially where the ground is uneven for any reason, since the bodies of the ants form bridges and make the path smoother. In addition, the workers form flanges at the edges of narrow lianas (figures 6 and 7) or on vertical surfaces, such as on the sides of trees. It is clear that these flanges and roadways are of considerable advantage when two or three large workers together must carry each of the larvae of reproductives which are twice the length of a single worker. The formation of these roadways is dependent upon workers bumping into and stepping on each other repeatedly. Near the end of the emigration when workers in the narrower column are no longer frequently stepping on the individuals at the margins of the roadway, these marginal workers are the first to move from their positions and join the emigration. Ant roadways are formed occasionally when a colony has a worker brood, but they are not as well developed. These roadways usually are close to the old bivouac where the traffic is heaviest and larvae are frequently dropped along the route. Sometimes an ant roadway will be formed for a brief distance when the queen comes to a part of the route where ants are having difficulty running. Short traces of roadways are formed occasionally along raid columns where there is exceptional activity.

"Guard workers" are frequently present but greatly scattered along the emigration columns. These are workers which face outward at the edges of the column and attack insects or other animals which may attempt to cross the column. A high proportion of these workers are majors. These guards when maximally excited keep their mandibles open wide, their antennae vibrate rapidly, and they rear upward with their front legs off the ground and their bodies almost vertical. Only workers which were not carrying booty or brood were seen to stop and act as guards. The length of time that these workers acted as guards varied from a few seconds to more than an hour for no apparent reason. In most cases, there also was no evident reason why there were guards in some places and not in others. However, any disturbance of the column results in an increase in guard workers. These guards were seen to attack beetles, sowbugs, spiders and other arthropods which attempted to cross the emigration column. In most cases the arthropod was not killed but retreated away from the column. The same arthropod that is readily killed during a swarm raid seems to have a better chance of survival when it runs into an emigration column. The ants which are laden have to be considerably disturbed before they will drop their burdens and attack. The guard workers will attack, but they seem slower and less effective than raiding workers.

When the queen approaches along an emigration column, the number of guard workers frequently but not always increases. The number of guard workers as well as the size of the "retinue", or group of workers which appears to accompany the queen, seem to depend primarily on the speed with which the queen travels. If her progress is not impeded by irregularities in the terrain, and she proceeds without hesitation, the retinue is small and there are no guard workers along the route in many places. However, if a bright light is directed at the queen and she halts, workers which are following her immediately start climbing over her and run ahead of her in a more excited manner. If she continues along the route after a brief pause, she will have a much larger contingent of workers accompanying her. These workers which make up the retinue are not the same small workers which are clustered around the queen in the bivouac. Larger workers and majors are common. The largest retinue which I have seen included between 25 and 50 majors plus a larger number of smaller workers which stayed within 15 to 30 cm. of the queen. Approximately another 100 majors were running back and forth and acting as guards as far as two meters from the queen. This queen was seen making good progress along the emigration column at a point ten to 15 meters from the old bivouac. The composition of the retinue may change to some extent as the queen progresses. The more the queen's progress is delayed, the more guard workers line the route. A similar reaction can occur if one has been collecting ants or myrmecophiles for several hours at one spot along the emigration route. The disturbed ants evidently deposit an alarm chemical which later excites the queen and other workers. Part of this reaction may be due to the "alarm" being passed from one worker to another as they reach this spot. However, on other occasions when no excited workers were noted running toward the old bivouac, subsequent workers seemed disturbed when they came to the point of observation.

Emigrations may be influenced considerably by chemical trails used previously around suitable bivouac sites by the same or different colonies. Schneirla and Brown (1950; 337) reported a colony followed an emigration route which it had used 31 days earlier. Colony '48 H-19 followed a trail more than 450 meters long made during the preceding week by colony '48 H-28. Another trail "approaching 40 meters in length made by colony H-15, E. hamatum, was employed by colony B-VIII, E. burchelli, after an interval of more than three weeks" (l. c.). These trails were also considered to last longer during the dry season than during the rainy season when more frequent wetting would be expected to wash the chemical away. Colony E-191, hamatum, emigrated on 19 June 1956 along what appeared for about 50 meters to be the identical route that colony E-159 of the same species had used on 11 May 1956. These two colonies also bivouacked under the same end of the same log. However, I had not marked the entire route of the previous emigration. Although it was clear that along major landmarks such as lianas and logs, the two colonies followed the identical route, in a few cases the second colony did not follow the precise route used earlier. Close to the bivouac, colony E-191 deviated and took the route that colony E-159 had used when it left that site. Since it is impossible to know how many chemical trails of army ants may be on any surface, or how frequently and recently they have been used, it seems best to be cautious when considering such cases of ants following old trails.

Regardless of the time when an emigration starts, there is a typical sequence of events which can be recognized in almost every emigration. These events will be discussed as they most frequently occur near the old bivouac. Closer to the new bivouac a similar sequence occurs except that the direction in which booty is carried may vary more if there are many branch columns in the vicinity of the new bivouac. Furthermore, the myrmecophiles are apt to be in less distinct groups. Theoretically, one could maintain that an emigration starts when the first ant leaves the bivouac at the start of a raid. However, since all these raiding ants also may return to the bivouac, the time when the first booty is carried from the bivouac is a more accurate starting point. Often a noticeable exodus of workers occurs before booty can be seen carried away from the bivouac. In all cases that I have observed, booty is first carried in both directions during this starting period. One reason that booty appears early in the emigrations is that much of the booty collected on the day's raid is concentrated in the bivouac near the raid columns. There may be considerable confusion along the column as ants with and without booty bump into each other and often reverse their direction. Sometimes a few workers with booty even try to return to the old bivouac more than an hour after the outward flow of booty and brood has begun. During this early period, myrmecophiles also are more frequently seen going in both directions along the column.

The next most obvious stage is the appearance of the brood. This is frequently preceded by a greater exodus of workers. When the brood consists of eggs or young larvae, it is almost impossible to see it. For this reason it is often advisable to take samples from the column approximately every half hour. If these samples are put into alcohol, the brood is usually dropped by the ants and sinks to the bottom. Myrmecophiles are common during the passage of the brood; and some kinds, particularly any which feed on the brood, may be more abundant than at any other time during the emigration.

Near the end of the brood or after the end of the brood, the queen usually is seen. Following the queen there is a gradual decrease in traffic, later a more rapid decrease near the end of the emigration. After the brood and queen have passed, there may be an increase in the number of myrmecophiles in the column. Booty may still be seen during this terminal period, and in the absence of brood it may be much more conspicuous than previously. The end of the emigration usually is quite abrupt, with ants decreasing from a column two to three ants wide to a trail without ants only five to ten meters away. The workers at the end of the column act in a manner similar to those at the beginning of a raid column, except that they are much less hesitant. They frequently run back in the direction of the old bivouac for a few centimeters and then turn and run after the rest of the column. After the last ant has passed the observation point, many more myrmecophiles may be seen following the trail. The species of myrmecophiles in this group may be different from any of those seen earlier in the emigration. Details on the species and abundance of the myrmecophiles will be given in a subsequent section.

Bivouacs of Eciton hamatum

The nests of army ants are called bivouacs primarily because they are much more temporary than the nests of other ants. The bivouacs are made up of the bodies of the ants which hang by their legs from some support. Several photographs of typical bivouacs can be seen in papers by Schneirla (1933, 1949b). The ability and tendency for the army ants to form hanging clusters seems to be unique among the ants. Other ants form piles of workers that may be many workers deep, but as far as I can determine, none will form "threads" of workers hanging together by their legs or large clusters of workers hanging from a support. Schneirla has repeatedly mentioned the "opposed recurved hooks" on the tarsi of the ants and stated or implied that these are "specific organic characteristics" necessary for forming this type of cluster (Schneirla, 1956b: 382; Schneirla, *et al.*, 1954: 293). However, most insects and probably all ants have "opposed recurved hooks". The only significant difference may be that the tarsal claws of army ants are slightly larger than those of most ants. They are not more recurved so far as I have observed. The tooth on the medial or lower margin of the claws is also not a necessary characteristic for this type of clustering. Other ants also have this tooth, and *Neivamyrmex* does not have it. In addition, the army ants appear to have relatively long and thick legs. Limited comparisons with ants of the same length, showed that the legs of the army ants in most cases were longer. When the other ants had legs of equal length, the legs of the army ants, especially the tarsi, were thicker.[1]

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[1] Borgmeier (1955: 16) discovered that all Ecitonini workers (and also *Acanthostichus* and *Cylindromyrmex*) have a yellowish stripe on the under surface of the hind tibia. This stripe varies considerably in length and width, but all workers have it. It is absent, however, on the males and queens. The texture of the surface of this stripe is different from the rest of the leg, and it also lacks hairs. Perhaps it is some kind of sensory structure. Although it is not known whether this unusual character has any connection with clustering or other behavior of these ants, its significance would bear further investigation.

Bivouacs are located usually under logs, in hollow logs or trees, between the buttresses of large trees, in underground cavities such as mammal burrows, in piles of brush, or similar places. Much has been written about the selection of bivouac sites, and many factors have been found to influence this selection. However, the relative importance of these factors is extremely difficult to estimate. Although the ants usually form their bivouacs in sheltered sites which are cooler and more moist than surrounding areas, the ants do not make a selection on the basis of temperature or humidity gradients. The selection is a more indirect one based primarily on the behavior of the ants and the mechanics of nest formation (Schneirla, Brown and Brown, 1954; Jackson, 1957). Toward the end of the nomadic phase and in the statary phase, there is a distinct shift to sites which are more sheltered and thus, cooler and more moist. The choice of site and formation of bivouacs are influenced by the following factors listed without regard for their relative importance. All these factors, except numbers 9 and 12, have been considered and in most cases discussed at some length by Schneirla, Brown and Brown (1954).

(1) Some support from which the ants can hang is apparently essential. This support also supplies some shelter. (2) Lack of disturbance by rain at the time of bivouac formation is important. If rain strikes a bivouac during formation or after it is formed, the ants may shift, depending upon the severity of the rain and the availability of a suitable site to which they can retreat. (3) Wind currents may be a crucial factor at the time of formation as well as after formation. Artificial currents will readily excite ants as they are starting a bivouac and cause breakdown of the initial ropes and clusters of ants. (4) Heat

(in the absence of light) will cause ants to move their clusters in the laboratory, but it is doubtful if this ever is important in the formation of bivouacs under the even temperature conditions on Barro Colorado Island. Bivouacs in hollow trees or logs may shift after they are formed, if sun heats the site considerably even though not striking the bivouac directly. Temperatures probably never are low enough on Barro Colorado Island to cause an adverse effect on the selection of a nest site. (5) Light similarly would not be a factor in formation of bivouacs at night, but it appears to cause shifts during the day. In the laboratory, ants will readily shift a cluster from a lighted part of a nest into a darker part. (6) Humidity normally is close to 90% at the time bivouacs are determined. Presumably if the colony nests in an area which is too dry, it will shift, if possible, to a more humid site. Colonies frequently form bivouacs at the ends of hollow logs. On the day following the emigration to these sites the colonies frequently shift deeper into the log. Humidity, light, air currents and temperature probably all play a part in these shifts. (7) Junctions in raid columns, where opposing traffic may become confused and the outward flow blocked, may result in accumulations of workers leading up to a bivouac. If outward traffic from the old bivouac meets strong inward or "centripetal traffic" (Schneirla, et al., 1954; 275), this may cause an accumulation of workers or a shift in traffic along a lateral branch column. Traffic may be drained along the lateral branch away from the initial cluster with the result that the final bivouac is formed along the lateral column. (8) Caches or deposits of booty and areas of greater booty odor result in workers stopping to feed, and the workers also drop larvae which feed on the booty. (9) Areas with considerable odor from raiding or emigration trails, as well as previous bivouacs of the same or other species of army ants may attract colonies to certain suitable sites. (10) The age of the brood or something correlated with its age probably influences the selection of the bivouac site. Colonies with more mature larval broods and pupal broods form bivouacs in more sheltered sites than colonies with young larval broods. (11) When the larvae are fully grown, the selection of a more sheltered bivouac site may be influenced by the availability of powdered rotten wood and similar detritus apparently necessary for spinning cocoons. Places where detritus of this type is more abundant typically are also more "sheltered" or "enclosed" (in the sense of Schneirla, et al., 1954: 273), and the sheltering is presumably more important than the presence of detritus. (12) The presence of the queen undoubtedly has some effect on bivouac formation and its coherence or stability (compare evidence in Schneirla and Brown, 1950: 330-331 on queenless colonies). Although a bivouac site is almost always determined and the bivouac probably over 90% completed before the queen reaches it, if the colony is divided between two sites, the part of the colony with the queen may become the final bivouac. Two bivouacs may be started in nearby sites, and if the queen stops in the first one, the ants in the cluster farther along the emigration route may return to the first site. Similarly, if the queen does not stop, but continues to the more distant site, the other ants are apt to follow her. Colonies deprived of their queens show varying degrees of bivouac breakdown and appear to have a weaker tendency to form a compact, undivided bivouac. (13) A bivouac will not be formed where there is a conflict with other colonies of army ants of the same or different species. Although actual fighting is rare between colonies of army ants, two normal colonies with functional queens are always to some extent antagonistic, and usually their raiding behavior would keep bivouacs apart. In a few cases where bivouacs of two colonies were observed in the same log, one colony moved out presumably because of disturbance due to the other colony. No disturbance by a nondoryline ant or other insect colony has been reported as causing a bivouac shift.

Once bivouacs are formed, major disturbances will cause shifts or complete emigrations depending in part upon the severity of the disturbance. A bivouac of either a nomadic or statary colony can be completely pulled apart and scattered around on the ground, and it usually is reconstructed on the identical site. However, if its previous support is partially or completely destroyed, the colony may move part of a meter or more than ten meters to a new site. Such a shift during the day will occur with statary as well as nomadic colonies. No shift of this type has been reported which was not due to human disturbance, but occasionally natural catastrophies such as floods, fires, etc., might cause similar shifts.

Schneirla has stated (1949b: 72), "... the fact that the bivouac-change processes often are more protracted and more variable in the dry months, with a greater lag in hitting upon the final bivouac site, indicates a greater scarcity than in rainy times of feasible clustering spots approximating the species optimum." No quantitative evidence was given to support this statement. However, in the same paper (p. 20-22) he gives the times when new bivouacs were started for colony '46 H-B during both dry and rainy seasons. These data show that the mean time for the starting of a bivouac was 7:05 p.m. during the dry season (dates from 12 February to 30 April), whereas it was 7:47 p.m. during the rainy season (dates from 2 May to 5 June). This also suggests that during the dry season the siesta period is not prolonged, and the emigrations may start earlier than in the rainy season. Perhaps the starting of new bivouacs is influenced by the time of sunset which on Barro Colorado Island would be about 30 minutes later in June than in March.

Refuse Deposits of Eciton hamatum

As a result of the kind of booty typically collected by hamatum colonies, there is little refuse around their bivouacs. Even at statary bivouacs only a trace of booty could be found. Where bivouacs touched the ground or the bottom of a hollow log, there usually were a few ants walking around possibly ten to 20 cm. from the edge of the bivouac. Occasionally four or five workers would be in a weak column extending 20 to 30 cm. from a bivouac, but these columns did not end in distinct areas of refuse. One or two of these ants were sometimes seen carrying booty refuse. Some scattered refuse could often be found, composed of the more sclerotized parts of booty, such as head capsules of older pupae. Empty cocoons from booty could also be found, but they were scarce possibly because many pupae had been removed from cocoons before they were brought back to the bivouac. On the last statary day empty cocoons of the army ant brood became obvious and rapidly increased through the first nomadic day. The ants carried some of the empty cocoons a few centimeters out of the bivouac along the supports of the bivouac or along the ground if the bivouac touched it. Apparently most of the empty cocoons were dropped by workers at the edges of the bivouac. Some cocoons drifted down to the ground directly; others got caught in the sides of the bivouac and probably did not fall to the ground until the ants emigrated. As a result the cocoons were generally scattered around on all sides of the bivouac and under the bivouac as well, if the bottom of the bivouac did not rest on any support.

Often Phoridae and Staphylinidae could be seen around the edges of the bivouacs. The staphylinids probably removed most dead workers. Additional details about the refuse from hamatum colonies will be given below in a section on refuse deposits and the arthropods associated with them.

Size of Colonies and Broods of Eciton hamatum

The size of any colony of army ants is difficult to determine, and colonies of the same species must vary by more than 100% in size, in view of the method of colony formation by division. Based on counted samples of 100 ml. of packed etherized or preserved ants in which worker counts can range from about 3,000 to 6,000, I would estimate that the size of hamatum colonies ranges from about 100,000 to 500,000 adult workers. Estimates based on emigrations probably are more accurate and tend to be somewhat lower than this.

Brood estimates vary even more widely, and it appears to me that the size of an individual brood may decrease markedly from the egg to pupal stages. Schneirla and his co-workers have emphasized that cannibalism may play an important part in the development of sexual broods (Schneirla, 1949a: 11; Schneirla and Brown, 1950: 334; Schneirla and Brown, 1952: 12, 29). However, in contrast to these broods of reproductives, "worker broods are produced without much evidence of cannibalism" (Schneirla, 1949a: 5). The extent of the cannibalism has not been well substantiated in sexual broods. The supposed greater extent of cannibalism when sexual broods are in colonies has been based partly on a decrease in the size of larval broods and partly on the finding of empty cocoons. It has been further suggested that brood consumption may be widely connected with production of new queens in the dorylines as well as in other ants (Brian, 1958: 500). However, I think that cannibalism of worker broods may also be extensive judging from impressions of the sizes of egg and young larval broods compared with mature larval and pupal broods.

Schneirla's estimates of the size of worker broods vary from about 20,000 (1948: 109), to 40,000 (1956a: 3), to 60,000 (1957b: 266) with no indication of the age of the brood involved. One colony of "about 30,000 workers" had a "counted 32,479 cocoons" (Schneirla, 1934: 321), which would seem to be an impossibly high proportion of brood. For comparisons with these estimates, Hagan (1954a, 1954c) determined that a burchelli queen has 2,528 to 2,644 ovarioles, each capable of producing 22 to 25 eggs per cycle. Thus, the total egg production would fall between 55,616 and 66,100 eggs during one statary period. The oöcyte number for hamatum was considered to be the same as in the queen of burchelli, but no ovariole number was determined (Hagan, 1954c: 4-5). My estimates of egg brood range from 50,000 to 200,000. Such large worker broods invariably seem to decrease in size perhaps to 10,000 to 60,000 at the age of full grown larvae.

Empty cocoons have also been found during statary phases of hamatum colonies with worker broods, but these cocoons were the same size and thus easily confused with those from nondoryline ants that are booty.

Perhaps there is considerable cannibalism by the recently emerged callows about which Schneirla writes (1952: 255), "During the first few days after their emergence they are confined mainly to the bivouac, where they feed voraciously and are almost incessantly in motion." Callows were definitely seen feeding on booty; how much they may feed on the army ant brood is unknown. In all large samples of brood, it was possible to find a few larvae of the army ants which looked somewhat shrunken or shrivelled. These looked the same as larvae on which the ants had been seen feeding in laboratory nests. Such larvae were difficult to spot in masses of brood, because they apparently were seldom torn apart by the ants until they were greatly reduced in size. The ants bit at them and apparently put small punctures in the larvae, and then fed on oozing juices. Sometimes no fluid could be seen to come out of the larva, but a worker would bite and lick it repeatedly. Since such larvae were never abundant, I suspect that most cannibalism occurs in the egg or youngest larval stages.

In one colony of hamatum, '55 H-E, workers during the statary phase opened at least several thousand cocoons when the worker pupae were still completely white. A sample of these pupae was examined, and no abnormalities were found among them. A physogastric queen had been removed from this colony on the previous day, and the bivouac had been considerably disturbed along with part of its support in the search for the queen. Perhaps this disturbance had initiated the tearing open of these cocoons. Opened cocoons and the pupae were not noticed the day when the queen had been taken, and most if not all of them must have been dropped below the bivouac within twenty hours of the removal of the queen. It is not known whether the workers ate any of the brood.

Presumably they fed to some extent in the process of tearing out the soft pupae. Similar disturbances of two statary bivouacs of hamatum, without taking the queens, did not result in attacks on the cocoons.

Because of the difficulty in estimating accurately the size of a colony, it is even more difficult to determine whether the colonies change in size. Schneirla (1949b: 18) states that colony '46 H-B was "noticeably very much smaller" at the beginning of a nomadic phase compared with its size at the end of the previous nomadic phase. This conclusion excluded the population of callow workers, but no mention was made of the population of full-grown larvae. The latter would cause the bivouac to look larger before the statary phase compared with after that phase with the same brood excluded. The same colony was followed long enough that four broods were added to its population, and still the population was "considerably less" than would be expected based on the addition of the broods to the initial population (Schneirla, 1949b: 25). This case is probably the best evidence for high mortality within the adult worker population. The most important factors limiting population size were considered to be "climatic hazards incurred in extra-bivouac activities" (Schneirla, 1949b: 76).

Sexual Broods and Colony Division of Eciton hamatum

Reproductives are generally produced during the dry season when some colonies have broods consisting at the time of emergence of about six queens and 1,000 to 4,000 males. It is not known whether the size of a colony influences the laying of reproductive-producing eggs during the dry season. Some colonies have been found with sexual broods at the same time that larger colonies had worker broods. However, other factors, such as the age of the queen and the food she received, or the dryness of the statary bivouac site may contribute to the production of a brood of reproductive-producing eggs rather than worker-producing eggs. Colonies with sexual broods have nomadic and statary phases like those of colonies with worker broods. However, there are many differences in behavior which have been reported primarily by Schneirla (1948, 1956a) and Schneirla and Brown (1952). Several of their most important findings will be summarized here.

Unfortunately there is only one record of a colony whose sexual brood was seen in the egg stage. The size of this brood was estimated as 15,000+ and as "quite as numerous as with a worker brood at the corresponding time" (Schneirla and Brown, 1952: 10, 12). Only an estimated 2,000 adult males developed from this egg brood. General impressions gained from sampling other colonies also convinced Schneirla and Brown that sexual broods normally are greatly reduced, not only during the larval stage, but also in the pupal stage. The much smaller size of the sexual broods compared with worker broods undoubtedly is an important factor in the rapid development of these male and queen larvae, in part because there would be more food available per larva. The total development time for sexual broods is about 43 or 44 days compared with 45 to 47 days for the worker broods (Schneirla and Brown, 1952: 17). However, the total volume or tissue bulk of the sexual broods may be considerably smaller than that of the worker broods (based on the estimated size of worker broods being more likely from 30,000 to 60,000, compared to 25,000 as estimated by Schneirla and Brown (1952: 12).

There is no doubt that the broods of reproductive larvae stimulate the workers more than a brood of worker larvae in spite of their smaller numerical size. Evidence of this has been given by Schneirla (1948) and Schneirla and Brown (1952). One aspect of this stimulation is the more frequent formation of "roadways" of workers along emigration columns.

Partly because of increased excitation of the workers and the antagonism between queens during the last two or three days of the statary phase, a bivouac with a sexual brood is apt to shift more than a bivouac with a worker brood. The queens emerge before the males, and the virgin queens may start to move away from the old queen and each other. They may move out of the bivouac and stay in the center of a cluster of workers adjacent to the bivouac.

The complex and highly variable process of colony division takes place during and directly following the emergence of the males. At this time the colony also has a young brood of eggs and larvae and will start a nomadic phase. A colony may or may not divide when it has a sexual brood, and the old queen may be superseded, or she may remain with part of the colony. It is probably impossible for a colony of hamatum to divide into more than two colonies, and colonies which do divide may not divide into equal halves. In all cases it appears that the two daughter colonies emigrate in opposite directions (i.e., the emigration routes form an angle close to 180° at the statary bivouac). A connecting column may remain between the two daughter colonies for a day, and if one queen is removed during the first few days after division, undoubtedly the two daughter colonies will fuse into one. For additional details see the paper by Schneirla (1956a).

At the start of the nomadic phase, immediately after the emergence of the males, each male along the emigration route is in or followed by a group of workers. The workers are in these groups not only because the workers are attracted to the males and cling to them in the emigration column, but also because the males have more difficulty running along the route and their larger bodies cause some blocking of the emigration column. On subsequent emigrations the number of workers with each male decreases probably due in part to a decreasing attraction for the workers. In addition, the males become stronger or more active with the result that they can shake off the workers by fanning their wings and can run away from the groups of workers.

Although the males are attracted to lights at night, they do not leave the bivouacs during the daytime. Most flights start along the emigration routes or at the old and new bivouacs during the emigrations (Schneirla, 1948: 100-101). The males are slow fliers with little ability to maneuver and no ability to defend themselves against predators. Few males of hamatum were taken at several lights on Barro Colorado Island during 1952, 1955 and 1956, even when colonies with alate males were known to be present on the island. The dates and times when males were taken during 1956 are as follows (with the number of males in parentheses): 9 May, 8:00 p.m. (1); 10 May, 9:00 p.m. (1); 29 May, 12:30 a.m. (1); 29 May, 9:30 p.m. (2); 3 June, 8:00 p.m. (2); 4 June, 9:30 p.m. (2); 29 June, 8:30 p.m. (1); 4 July, 9:00 p.m. (1). These dates can be grouped into three pairs of consecutive nights and a final pair five days apart. Probably all the males came from three or four or at most six colonies.

The males probably are not capable of mating for about three days after their emergence. A flight may also be essential before the males can mate (Schneirla, 1948: 107-108). Therefore, males probably cannot mate with queens from their own colony during the first few days or a week after the queens have emerged. This allows time for fertilization by males from other colonies, if there are any with sexual broods near by. However, if no other males are in the vicinity, the probability increases that after they have flown, males from the same colony will mate with the queens. Following the flight from the parent colony, the males soon lose their wings. The genitalia also may become somewhat more protruded, but they have never been seen as widely spread as in males of Labidus and some other army ants. Within two weeks of their emergence, almost all males have left their parent colony. Their scarcity in other colonies and the short periods when the males were taken at lights are evidence that the males die within one to three weeks after emergence. The fact that I have never seen a male army ant of any species with frayed wings further supports the hypothesis that the males are short-lived and weak fliers.

Activity Cycle of Eciton hamatum

The activity cycle of alternating nomadic and statary phases was first described by Schneirla (1933), and all his papers on army ants since that date contain some information related to this cycle. A diagram of the cycle is given in figure 63. With a worker brood, the nomadic phase is typically 17 days, but may range from 16 to 18 days regardless of rainy or dry seasons. The statary phase ranges from 18 to 22 days. However, the mean for this phase during the rainy season is 19.6 days, and the mean in the dry season is 20.3 days (Schneirla 1957a: 107). Because of the confusion of dry and rainy season records published by Schneirla (1949b) and Schneirla and Brown (1950), these means should be computed again. With a sexual brood, the length of the nomadic phase is considerably shortened to eight to 13 days, but the statary phase remains about the same length (Schneirla and Brown, 1950: 322-323).

The initial emigration beginning a nomadic phase has been attributed primarily to the stimulation of the older workers by the newly emerged callow workers. These callow workers emerge almost exclusively on the last statary day and first nomadic day. It is rare to see a cocoon being carried on an emigration on the first nomadic day, and none could be found when this entire emigration of colony E-121 was watched. The new brood of eggs and young larvae are considered to be of negligible importance for exciting the workers at this time. The callows have been considered "hyperactive and voracious" (Schneirla, 1944c: 181), but samples from two colonies which I have watched did not show these characteristics. (This does not imply that they do not or could not arouse the workers adequately for an emigration.) For the most part the callows stay together in large groups in the bivouac. They do not take part in the raids of the first statary day and are found in considerable numbers in raids only when they are approaching the color of the older workers about five days after emergence.

As the stimulation of the workers by the callows decreases, the stimulation by the larvae theoretically increases, maintaining the large daily raids and nightly emigrations. The brood of eggs and young larvae is in relatively tight clusters covered with minor workers. As the larvae increase in size, they become more active and more widely distributed throughout the bivouac, and additional workers come in contact with them.

The daily raids during the nomadic phase are clearly larger on the average than those during the statary phase. Schneirla has further reported that larger raids occur and the emigrations are longer near the end of the nomadic phase compared with the beginning (1944c: 182). No supporting quantitative evidence has been presented to demonstrate these differences. When raids and emigrations were observed, it appeared to me that the size of the raids, but not necessarily their maximum distances from the bivouac or the distances between bivouacs, increased during the nomadic phase. Moreover, the emigration distances for one colony, '46 H-B, did not show such an increase when they were graphed (see figure 73). This graph shows a slight decrease in the emigration distances at the end of the nomadic cycle for this colony, which was studied for a longer period than any other colony. The mean distances for these emigrations, grouped by pairs starting with nomadic days one and two, and not counting the 17th nomadic day in the second cycle, are: 130, 133, 183, 162, 179, 143, 132 and 161 meters. Using the method of moving averages (mean distances for days one to three, two to four, etc.), one can compute the following means: 138, 150, 144, 155, 176, 172, 159, 173, 179, 163, 154, 123, 146, 137 and 146. Both methods indicate slightly longer emigrations in the center of the phase. Moreover, the short emigrations of 120, 30, 110 and 15 meters occurred respectively on the 10th, 12th, and twice on the 14th nomadic days which are all before there is appreciable spinning by the larvae.

As mentioned above, colonies at the end of the nomadic phase more frequently form bivouacs in enclosed or more sheltered sites. Common bivouac sites are inside hollow logs or holes in the ground. During the last nomadic day and first statary day, larvae are carried out of the nest for spinning. As the larvae spin cocoons, the resulting drop in stimulation of the workers initiates the statary phase.

During the statary period raids are much smaller and less frequent, and on some days there may not be a raid. The bivouac stays approximately in the same place, but there always is some shifting of its exact position. The bottom of a statary bivouac of colony '46 H-A inside a hollow tree varied up and down through a height of 18 cm. from day to day (Schneirla, 1949b: 40). Part of this shifting may not indicate any movement of the center of the cluster, but rather an addition or subtraction of ants around the periphery as the ants leave or return from raiding. On other occasions the entire bivouac has been seen to shift one to three meters deeper into a hollow log. I have seen an actual shift in progress on only one occasion. In this case the ants had an "emigration" column between the two bivouacs about a meter apart, and the queen must have run along this column. In other cases it is possible that the bivouac may have shifted by the addition and subtraction of ants from opposite sides of the bivouac over a period of several days, rather than by having a complete movement of the entire colony along a column. Some shifting of the bivouac may be important to give relief to those ants making up the major supporting walls of the bivouac. In three cases a colony of hamatum moved more than five meters during the statary phase, but these moves followed considerable destruction of the original bivouacs and their supports.

At the end of the nomadic phase, the queen may show slight traces of physogastry, but during the first week of the statary phase her gaster apparently reaches its maximal size (Schneirla, 1957a: 118). Presumably the eggs are laid primarily during a week in the middle of the statary phase (of 18 to 22 days). Unfortunately, there appears to be no reliable data to indicate the beginning and end of the egg laying period. Eggs have been laid in laboratory nests at a rate of 178 per hour for a seven hour period (Schneirla, 1944c: 167). At this rate the queen could lay about 43,000 eggs in ten days. This total approximates those of other brood estimates.

Throughout Schneirla's many papers it is repeatedly emphasized that the brood is primarily responsible for the activity cycle because of the brood's stimulation of the workers. Before the work of Schneirla, it was thought that the ants exhausted the supply of food in the area of the nest and then were compelled to move to find additional food. Abundant evidence against this simple hypothesis has been given repeatedly by Schneirla. Nevertheless, as Schneirla (1957a: 121-122) has also pointed out, emigrations are a necessary adaptation, since army ant colonies are too large to be able to find adequate supplies of food within the restricted areas around their nests for a long period of time. One aspect of this problem which has not been adequately studied is the quantity of booty which is brought in to the nest and how this may affect the distance and duration of the raids and the length of the emigration. Emigrations vary in length from a few meters to several hundred meters for no apparent cause. The influence of the abundance of food on the direction and distance of raids and emigrations can be seen most clearly when the ants find an especially rich source of booty, such as a large wasp nest, and increase their raiding to that source. They may subsequently form a large booty cache and a bivouac at that spot. However, when the ants appear less successful, it is more difficult to determine whether the distances of the raids and emigrations are affected. In addition, the behavior of the larvae may be directly related to the abundance of food. No data are available to indicate whether larvae which are well fed are quieter and thus stimulate the adults less than hungry larvae. Such a relationship might be predicted on the basis of other species of insects.

Interrelations Among Individuals of Eciton hamatum

Adult workers rarely exchange food or secretions by their mouthparts, but they frequently clean or lick each other's bodies. An individual worker also licks its own body with its maxillae and labium. Although no quantitative measurements were made, it appeared that most of this cleaning was concentrated on the tip of the abdomen and the front legs.

There was no indication that any of the workers were attracted more to majors or cleaned majors more than they cleaned smaller workers. However, adding a major to a dish of workers caused more excitement than adding a submajor or smaller worker. This was not true if a small worker was taken from a dish with a queen and added to a dish of workers without a queen. Workers which had been with the queen apparently carried some queen odor which greatly excited the other ants. Brown (1960) has reported some evidence that a chemical, possibly from the mandibular gland, is released from the heads of majors. This chemical alarms and attracts other workers which will attack the head of a major when it is severed from the ant's body. These majors may be adapted for alarming the rest of the colony, but all workers seem to have this same ability, if to a lesser extent. The majors alone possess large, shiny heads with elongate, hook-like mandibles, and there are no intermediate shapes between these and the more triangular mandibles of the submajors. The majors readily would sting and bite prey, but they were never seen to carry any booty or brood.

No major or submajor was ever seen being carried by another worker. Moreover, there appeared to be an inverse relationship between the size of the workers and the extent that they were carried. The youngest callows were also carried much more than older callows and dark workers, and more workers were carried at the ends of emigrations than at any other time during raids or emigrations. In numerous cases these pairs of workers have been aspirated from columns. As soon as they were aspirated into a vial, both workers would run around actively, and there was never any sign that one of them was injured. The only time the two could be distinguished was when one was different in color or size from the other. No callow worker was ever seen carrying any other worker. Perhaps only slow, quiet workers are picked up by the more active individuals. In this way workers that are lagging behind at the old bivouac are picked up and carried along by other workers. The smallest workers which are carried most frequently are also the slowest moving and the last to emerge from cocoons.

The workers seemed to be more attracted to callow workers than to other older workers. Not enough observations, however, were made to reach any strong conclusions. The mature workers assist the callows to emerge by tearing the cocoons. Callows also emerged from cocoons isolated from workers, but considerably fewer emerged in a given time and more died in their cocoons. After the callows have emerged, they show a distinct tendency to stay together. When bivouacs containing callows are broken open during the first or second nomadic day, the callows to a large extent are concentrated in large masses. After several days they become completely integrated throughout the colony. Schneirla (1944a: 3) has also reported that there is a gradual appearance of the callows in the raid columns during the first five days of the nomadic phase. In the laboratory young callows usually die before older workers. Among the older workers the smallest individuals generally die first, and the majors are the last to survive. Under more adverse conditions the same relationship holds, as shown by Schneirla, Brown and Brown (1954: 283) for workers kept in a box at a relative humidity below 60%

As shown in the discussion of sexual broods, the workers are considerably attracted to the callow males, the attraction decreasing over a period of several days judging from the number of workers on each male. Queens which are callow may or may not be more attractive than old queens, judging from the results of colony divisions where old queens are sometimes superseded. Presumably the relative attraction of the various queens at the time of a colony division determines which queens survive in the daughter colonies (Schneirla, 1956a: 54-55).

Army ant queens invariably die when separated from their colonies. All queens which had been kept in the laboratory with a few hundred workers or less died within ten days, and about half of them died within four days (Schneirla, 1944c: 171). A queen kept "with her colony for more than two weeks in the laboratory" died within four days after she was segregated with a small group of workers. Queens with their colonies can live in the field at least four and one-half years (Schneirla, 1956b: 402).

When a queen was found in a bivouac, she typically was surrounded by a tight mass of workers which remained around the queen in a laboratory nest, making it impossible to observe her. When only about ten workers were placed in a dish with a queen, the queen normally was much more active than she was with the larger mass of workers. Workers followed her as she ran about the dish, and they frequently rode on her abdomen or thorax. After one or two days fewer workers stayed on or close to the queen. The workers licked the gaster of a queen more frequently than any other part of her body and never were seen to feed a queen or touch her mouthparts with their own. Moreover, no queen was ever seen to feed independently in laboratory nests, although on a few occasions she appeared to drink a little when crushed booty or cotton soaked in water was held against her mouthparts with forceps. Schneirla also reported that the workers were more attracted to a physogastric queen than to a contracted queen (1944c: 169). When the queen is laying, small drops of "fecal material" are deposited between the spurts of eggs. These are "evidently much relished" by the workers (*l.c.*). I have never been able to determine the source of these drops when watching physogastric queens of *hamatum* or other species. Perhaps the drops are not fecal material.

Workers sometimes spent more than an hour resting on the gaster of the queen in laboratory nests. These workers frequently licked the abdominal terga, and records were kept of the number of times workers licked or kept their mouthparts over the individual terga. With the queen and workers running and turning frequently, it was difficult to tell how often the workers were actually licking the queen. Therefore, the counts are based on the positions of the heads of the workers. Workers were recorded only if they remained in a given position for at least two seconds. The same ant was not recorded more than once, unless it had moved away from the queen or shifted its position to a different segment. The queen was moving intermittently so that the workers frequently shifted position or were brushed off. Ants with their heads over the junction between two terga were recorded with the more anterior tergum. By this method an ant in a position for two seconds was recorded with equal value to one there two minutes. In spite of their limitations, these data do show a differential attraction in the case of a contracted queen (E-123). The frequencies were measured over a period of two hours and were recorded as the number of ants per segment (see table 2).

Several conclusions seem to be warranted as a result of the above observations. The workers showed no indication of an attraction to the anal region of the contracted queen (even when she remained stationary for several minutes). They rested most frequently with their mouthparts over the first and second gaster segments and especially at the junction between the first and second segments. This position undoubtedly results in part from the fact that a worker can more easily ride on the larger and more level anterior segments of the gaster of the queen than on the more sloping posterior segments. The workers seldom rode on the queen facing posteriorly. When they did ride in this position, they usually were standing on the thorax or petiole with their mouthparts over the first or second gaster segments. In addition, the workers on the floor of the dish kept their mouthparts (or heads) close to the first and second terga most of the time. Probably the chemical which is responsible for the attraction to the queen is secreted from glands at this part of the gaster. However, these data are considerably different from similar records for two other queens as can be seen in table 2.

Hagan (1954b: 14-16) reported that two pairs of glandular cell masses were segmentally arranged "in the vicinity of the vulva" of a hamatum queen. Each mass consisted of approximately 50 cells, each of which has one ductule extending through the exoskeleton. The opening of the ductule is enlarged and apparently surrounded by small setae. Hagan wrote, "It is quite possible more of these glands are present in other segments, but only the two pairs were observed." His investigation was primarily concerned with the reproductive system, and no information was given on the body wall or glands of the anterior part of the gaster.

Schneirla (1944c: 163) has reported, "Workers are especially attracted to pieces of cardboard formerly in use as floors for the queen's cell, and will collect in the one of two compartments in which a queen has rested for a time." This reaction may be due to a queen odor, but no adequately controlled experiments have been done.

Workers will stand on top of a pile of larvae for more than a half hour without moving or licking them. At other times the squirming movements of the larvae seem to attract workers which are standing on or near them or running over them. These workers may then shift the larvae or may lick them. Since the larvae are extremely inefficient at crawling across even rough surfaces, it is essential that the adults bring food to them or take them to food. The workers apparently feed the newly hatched larvae while licking them. However, the older larvae seldom if ever are fed directly from the mouths of workers. The adult ants pile booty on top of the larvae and larvae on top of booty. The larvae are frequently found inside sclerotized pieces of booty, such as head capsules or legs where the adult ants would not be able to feed.

It has been suggested on the basis of the reduction of the proventriculus (Eisner, 1957: 478, 485; Eisner and Brown, 1958) that the adult dorylines may eat solid matter. However, their method of feeding indicates that only liquid food is usually ingested. The mandibles were seen to be used when an ant was pulling or tearing food, but they were never used like those of a grasshopper for chewing food. The reduction of the proventriculus is more apt to be connected with the weak development of trophallaxis.

An adult carries a larva by holding it usually near the anterior end and only occasionally near the posterior end. The worker's mandibles usually grasp the first or second thoracic segments of the larva. Because the anterior end of a larva is narrower than the posterior end, workers may find the anterior end easier to grasp. However, these workers can easily carry larvae with a larger diameter, and it appears that the workers are attracted to the anterior end probably by chemical rather than morphological factors.

When the larvae are fully grown, the adult workers carry them out of the bivouac to areas of fine loose detritus, such as powdered rotten wood. There the larvae spin their cocoons in the loose surface layer. When the cocoons are nearly or completely finished, the workers grasp the cocoons near the narrower posterior end and carry them back into the bivouac. In laboratory nests the cocoons are ignored more than larvae, but the workers will often pile them in one place and stand on top of them. Schneirla (1944c: 177) reported "they are presumably neutral in importance or may actually exert a quieting effect upon the workers that clutch them in their mandibles, somewhat as the pressure of thumb-in-mouth pacifies an infant." When the callows are ready to emerge, their movements appear to attract workers which then help the callows to get out of the cocoons.

Eciton lucanoides Emery

Eciton lucanoides Emery has been divided into two subspecies, *lucanoides* *s. str.* and *conquistador* Weber, by Borgmeier (1955: 262-269). However, since the males of both subspecies and the queen of one are unknown, there is a strong possibility that these are two distinct species. A total of 24 specimens from only four samples of the former subspecies from Peru, western Brasil, and Bolivia were examined by Borgmeier. The latter subspecies is known from about ten colonies found in Costa Rica and Panamá (including Barro Colorado Island). Although these few records indicate the species is generally rare, Schneirla and Brown found two colonies, compared with three of *hamatum* and one of *burchelli*, "during a five-day survey of the forested Candelaria area above the confluence of the Pequeni and Boqueron rivers" [*Panamá*] (Schneirla, reported by Weber, 1949: 5). On Barro Colorado Island all collectors have apparently found only one *lucanoides* colony out of over 500 colonies of *Eciton*.

Biological observations have been made only on the subspecies *conquistador*. The two colonies found by Schneirla and Brown had column raids which were quite strong between 11:00 and 11:30 a.m. However, *lucanoides* is considered to have raid columns that are "characteristically narrower than those of *hamatum* and both in width and in the behavior of workers on them are roughly transitional between *hamatum* and *rogeri*" [= *mexicanum*] (Schneirla, reported by Weber, 1949: 6). *E. lucanoides* is similar to *hamatum* but somewhat darker in color. The two species would be easy to confuse in the field. Consequently, whenever weak columns of *hamatum*-like army ants are found, especially at night, one should examine the ants carefully to see if they are *lucanoides*. Their food also appears to be the same as that of *hamatum* (*l. c.*).

Only one emigration of *lucanoides* has been described (Nevermann, reported by Reichensperger, 1934: 241). Larvae were carried during the middle period of this emigration, and the queen was taken in a cluster of workers after all the brood had passed. Following the queen, some staphylinids were seen about 11:00 p.m., and at 11:30 p.m. the column ended. Thus, as would be expected of a primarily subterranean species, this emigration was later than the average *hamatum* emigration. Schneirla and Brown (1950: 313) reported one colony emigrated about 140 meters, but they did not watch this emigration.

Bivouacs have been found in three hollow trees, one hollow log and in the dense crown of a fallen tree (Schneirla, reported by Weber, 1949; Borgmeier, 1955; 265; and Nevermann in Reichensperger, 1934: 241). These records indicate that the bivouacs were in well-sheltered but nonsubterranean locations. The three nests for which dates are given were all found between 27 October and 15 November during the height of the rainy season. The species has distinct broods and probably has an activity cycle similar to that for *hamatum*. No sexual brood has been found.

The meager data above from raids, bivouacs and one emigration suggest that this species is approximately as epigaeic as *E. vagans* and less epigaeic than *hamatum* and *burchelli*.

Eciton burchelli (Westwood)

E. burchelli and *hamatum* apparently have identical ranges, except the latter species has not been found on Trinidad. Although Borgmeier (1955: 183-192) did not separate *hamatum* into subspecies, he divided *burchelli* into the following subspecies: *burchelli* *s*. *str*. (from Brasil and Paraguay), *foreli* Mayr (Honduras, Costa Rica, Panamá, Colombia and Ecuador) *parvispinum* Forel (México, Guatemala, Honduras, Nicaragua, Costa Rica and Panamá), *urichi* Forel (Trinidad) and *cupiens* Santschi (Colombia, Venezuela, British Guiana, French Guiana, Brasil, Perú and Bolivia). Among these localities given by Borgmeier, there are several cases in which two subspecies are sympatric over considerable areas. Additional collecting will have to be done before an accurate description can be made of the variation within the species. Specimens from Barro Colorado Island and parts of Panamá south and east of the Canal Zone are *burchelli* *foreli*. Specimens from Chiriqui are *b*. *parvispinum* (Borgmeier, 1955: 189).

Raids of Eciton burchelli

E. *burchelli* feeds on a greater variety of food than any other species of *Eciton* observed on Barro Colorado Island. Even though the amount and kind of prey which *burchelli* captures is influenced largely by its manner of raiding in swarms, the behavior of the individual workers is also of great importance. The workers seem more easily excited, quicker to attack and more pugnacious, and they have a stronger bite and a more potent sting (to a person) than any other species of *Eciton*. Their method of raiding by large swarms (discussed more fully below) results in their driving numerous animals out from under leaves or other objects. A column raid is much less effective in flushing out animals, primarily because the ants cover a much more limited area in any one vicinity during a short space of time. Any animals flushed out by a column raid would be able to escape the ants by moving a relatively short distance away. Animals must run or fly a greater distance to escape the onrush of the ants in an advancing swarm front two to 15 meters wide.

When one first watches a swarm raid of burchelli progressing across the forest floor, it appears that the ants kill all kinds of arthropods. Unfortunately, a thorough survey of the food of any species of army ant has never been made even from a qualitative standpoint. Careful observation, however, revealed that along the ground, as in the trees, burchelli killed more ants than any other group of arthropods. Wasps, Orthoptera (s. lat.) and spiders were probably next in abundance among the booty. However, a large proportion of the potential prey of the forest floor always seemed to escape. Even when the ants attacked nests of social insects, although the brood was completely killed, most of the adults escaped. Some arthropods were never attacked, and casual observations indicated that 30% to 50% of the arthropods attacked escaped being killed. Most of these arthropods avoided capture by running away in front of the swarm, flying, or climbing up vegetation. Others ran or jumped to a spot in the middle of the anastomosing columns behind the swarm front. If they landed between columns, the ants sometimes did not find them. However, if they landed on a column or in the midst of the swarm, they almost invariably were killed in a few seconds. As Schneirla (1945: 176) has pointed out, even burchelli colonies do not come close to depleting the supply of prey around a statary bivouac, and any area cleared of prey may be rapidly repopulated.

The raiding workers attacked almost anything that moved, including a blade of grass, a vertebrate or an arthropod. The movement of the object was of prime importance since the ants attacked a blade of grass only when it vibrated, and they immediately ceased attacking it after one or two bites. Many times an arthropod was seen to escape being killed when it remained motionless. The same species, on other occasions when it moved, was promptly killed. The importance of the movement of the prey can be demonstrated by vibrating or shaking a tettigoniid or cicada in the area of the swarm. Before the vibration, the insect may have been ignored, but with the vibration the ants quickly attacked the insect and continued to attack it as long as the vibration persisted. The motion of the arthropod was undoubtedly not the only factor here. The ants varied greatly in the speed, intensity or efficiency of their raiding and were usually much less efficient than at the height of a maximal raid. Probably the number of workers around any potential booty object also was important in that 100 workers appeared more than twice as efficient in attacking as 50 workers possibly due to mutual stimulation among the workers.

There are no records of burchelli eating any plant material, not even vegetable oils and nut meats, which are eaten by some other dorylines. Vertebrates will be attacked if they persist in staying in the swarm of raiding ants. I have seen mammals like the tapir (Tapirella bairdii), anteater (Tamandus tetradactyla) and coati (Nasua narica) being driven out of areas where they were feeding by swarm raids of burchelli. The tapir has a tough skin, but it is vulnerable to bites or stings between its toes. The coati and tamandua eat other ants, but not the army ants.

Once a small dead snake was found at 9:30 a.m. in a mass of burchelli about three meters from the bivouac. Probably the ants had killed it a few hours earlier at the start of the raid. During the two hours after the snake was first seen, hundreds of workers bit and pulled on the snake and managed to tear it partially open. During those two hours the ants had clearly been successful at eating a small part of this snake. On the following morning the completely stripped but intact skeleton (38 cm. long) was found in the same spot, but it is not known how much of the snake was eaten by the burchelli and how much was eaten by other ants or insects. Although this is the only time that I have seen a vertebrate which was probably killed by army ants, iridescent blue lizard tails about six centimeters long were seen occasionally in the raid columns. Presumably the lizards usually escaped; at least no other parts of them were seen being carried back to the bivouacs. No other pieces of vertebrates were ever seen being carried in ant columns, nor were they found in refuse deposits.

Since burchelli raids up into the tops of the tallest trees, one would suspect that they may frequently kill nestling birds. Schneirla (1956b: 389) states, "I have seen snakes, lizards, and nestling birds killed on various occasions; undoubtedly a larger vertebrate which, because of injury or for some other reason, could not run off, would be killed by stinging or asphyxiation. But lacking a cutting or shearing edge on their mandibles, unlike their African relatives the 'driver ants' these tropical American swarmers cannot tear down their occasional vertebrate victims."

The mandibles of ecitonine workers, other than the Eciton majors, work like pliers which clamp on the prey. The mandibles do not cross or overlap more than a slight amount at their tips, and they have a poor toothed cutting edge. The mandibles appear to function more like wire cutters with edges which abut. All the booty is primarily pulled apart with little actual cutting, although a worker may gnaw at one spot for more than 15 minutes. The mandibles of *Dorylus* (*Anomma*) are long and curved with much sharper toothed cutting edges which overlap and apparently cut like scissors. *Eciton burchelli* and all other Neotropical army ants cannot strip flesh from vertebrates or are much less efficient than *Dorylus (Anomma)* at such action primarily because of these differences in the mandibles.

Both *hamatum* and *burchelli* attack the nests of many species of Polybiinae and Polistinae (Vespidae). However, *burchelli* kills a greater proportion of the adults; and since it goes higher into the trees, it must prey on some species that are above the level of *hamatum* raids. Likewise, *burchelli* more frequently raids ant colonies in trees, especially *Camponotus sericeiventris* (Guerin), the largest carpenter ant on Barro Colorado Island. The largest ponerine found there, *Paraponera clavata* (Fabricius), is also frequently attacked by *burchelli*, which is successful at killing the workers in subterranean nests even though these ants are about twice as long as the largest majors of the army ant. When various species of ants were raided by *burchelli*, it appeared that they often made almost no attempt to resist the army ants. Other ants, such as species of *Atta* and *Cryptocerus*, either were not attacked, or they resisted strongly and were rarely killed even though they are smaller than the *Eciton*.

When either *burchelli* or *hamatum* attacked a colony of wasps or nondoryline ants, many of the adults of the attacked species, and especially the returning foragers, were seen around the periphery of the nest or resting on near-by vegetation. One would expect that the swarm raid of *burchelli* would be more successful than the column raid of *hamatum* at capturing some of these insects displaced from their nests.

Pieces of Orthoptera are among the most frequent prey which can be identified in raid columns. Blattidae, Gryllidae and Tettigoniidae are the most common families killed. Hemiptera may or may not be killed, possibly dependent in part upon their abdominal scent glands. Coleoptera are frequently attacked, but often the ants are incapable of killing the larger and more heavily sclerotized species. Beetles such as Scarabaeidae, Carabidae and Elateridae normally retract their legs and remain motionless. The ants frequently pull off all the tarsal segments and then abandon the beetle.

Schneirla (1956b: 389) reported that walking sticks taken on bushes in Trinidad in daytime (Schn. 1961 pers. com.) [Phasmidae] are not killed because of "repellent chemicals, as tests show, as well as through tonic immobility." Four phasmids were promptly killed when I attempted to repeat this experiment in the laboratory. All the specimens were too badly fragmented to be determined, but at least two species of wingless phasmids were killed.

Odonata are rarely killed, as one would predict. Nevertheless, around the statary bivouac of colony '55 B-IV, I picked up 120 wings of dragonflies (Anisoptera). Evidently at least 30 dragonflies had attempted to rest under the log where the ants were clustered and had been caught when they touched the bivouac. In a similar manner, burchelli may kill a fair number of insects such as Diptera and Hymenoptera which one would not expect the army ants to be able to capture.

Ticks were reported by Schneirla (1956b: 389) to be immune from attacks. All the ticks which I have observed with burchelli were Ixodidae, and none of the ants attacked any of the ticks. It did not make any difference whether the ticks were gravid or ungravid, nymphs or larvae; the ants ran up to the ticks and then turned away. Perhaps the coxal glands of the ticks secrete a substance repellent to the ants. However, in laboratory nests burchelli was seen to walk on two ticks and no repelling of the ants was observed.

Numerous species of spiders and especially Lycosidae, which are common on the forest floor, were killed by burchelli. No tarantulas were seen killed, nor were their remains found in refuse deposits; however, Schneirla (l.c.) reported that they are killed. On several occasions, tarantulas were seen to lift their legs in succession and shake burchelli workers off of them. Other spiders occasionally escaped by hanging down from plants by silk threads when raiding ants drove them off the plants. Scorpions were frequently killed, but the whipless whip-scorpions, Tarantulidae, always darted out of the path of the ants and even were observed to eat burchelli workers.

Termites also seem to be largely immune from attack (Beebe, 1917: 521; Schneirla, 1956b: 389), but a few termites were found among booty. Perhaps only occasional foraging termites are captured since the army ants were not seen to attack numerous termite nests in the areas of the ant raids.

On the basis of the fragmentary but numerous observations given above, it is evident that Eciton burchelli is selective in its feeding. A thorough study would undoubtedly reveal many other arthropods which are not attacked or not eaten by these ants. E. hamatum and other species of army ants appear to be even more selective than burchelli.

Swarm raids of burchelli start near dawn when hamatum raids begin. However, their inherent differences are immediately apparent. Workers swarm out in all directions from the bivouac of burchelli and quite thoroughly cover the ground. The raiding workers within fifteen minutes have started to narrow down the swarm to one or two primary directions. Usually within the next hour the swarm is further directionalized and has the form shown in figure 70, except that it is smaller. Maximal raids reach their peak about 11:00 a.m. when they are approximately the size shown in figure 70. The swarm front may shift to one side or another as it progresses across the forest floor, but usually it maintains a fairly constant direction. If a particularly rich source of food is found at one edge of the swarm, a smaller subswarm may advance in that direction. At other times, the main swarm may shift toward the source of booty. If the swarm comes to a tree, it may or may not go up the trunk. Perhaps chemical trails of other colonies or species of army ants or other insects attract the swarm up these trees. A raid swarm will go more than ten meters up the largest trees even though little booty will usually be found in the region of the main trunk.

A continuous column of workers running in both directions connects the raid swarm with the bivouac at all times. The base column is usually three to 12 ants wide, or about twice the width of the base columns of *hamatum* raids. As with *hamatum*, there is a siesta period of decreased activity followed by an afternoon resurgence leading up to an emigration if the colony is in the nomadic phase. During the siesta period or at any time when the raid is greatly diminished, the swarm pattern becomes much less obvious. At these times the swarm of ants may cover only about a square meter of the ground, and in some places the ants appear to be column raiders. The swarm makes little progress, and a high percentage of the ants may be moving in the direction of the bivouac. The various factors connected with the broods which influence the size of *hamatum* raids, also affect the raids of *burchelli*. Raids of *burchelli* at their maximum development never extend as far from the bivouac as the raids of *hamatum*. Judging from the decrease in the size of a bivouac after a raid is in progress, both species of *Eciton* have approximately the same proportion of the colony taking part in a maximal raid. Since the colonies of *burchelli* are at least twice the size of those of *hamatum*, the number of ants on the raids must be correspondingly greater. Unlike *hamatum* which usually has raid columns extending in two or three directions when it has a large raid, *burchelli* usually has a single raiding system in one direction.

It has been reported by Schneirla (1949b: 74) that *burchelli* is less apt to raid during the statary phase in the dry season than in the rainy season. The decrease of 14% in the number of days with raids was based on one colony which had a sexual brood, and that brood might have been more responsible for the decrease than the dry season itself. A more valid comparison would be based on the number of colonies raiding on the individual days of the statary period. Some decrease in raiding may occur during the statary phase in the dry season, but no adequate quantitative data are available.

The swarm raids of *burchelli* differ markedly from column raids of other species of army ants in the large number of birds and flies that accompany the ants. There are about ten species of antbirds which commonly follow the swarm raids of *E. burchelli* on Barro Colorado Island. A brief study of the behavior of these birds around the swarm raids has been made by Johnson (1954). The two species of antbird which are present over most swarms are the Bicolored Antbird, *Gymnopithys leucaspis*, and the Spotted Antbird, *Hylophylax naeviodes*. These appear soon after the raid starts and follow the swarm front as it advances. The calls of both of these species are a repeated low "cherr" or "churr". These calls are useful indicators of the location of swarm raids of either *E. burchelli* or *L. praedator*. (Bates [1863 v. 2: 357] also reported antbirds over *E. drepanophorum*, but there are no subsequent reports on the type of raids of this army ant.) Dr. Alexander Wetmore, who has studied birds for many years in Panamá, has told me that he has repeatedly and only found swarm raids of army ants by tracing the calls of the antbirds.

These antbirds primarily feed on insects escaping from the ant raids rather than on the army ants (Johnson, 1954: 44; Schneirla, 1956b: 390). However, there is evidence that some of the birds accompanying the swarms do feed to a considerable extent on the army ants. Ihering (1912: 235) reported that the stomach of one specimen of *Neomorphus geoffroyi* which had been accompanying a swarm raid of *E. burchelli* was filled with the army ants. There is some additional evidence that some of the antbirds may feed on the army ants (Bequaert, 1922; Wheeler, 1932: 307). Nevertheless, most of these birds do not eat the army ants, or if they do eat them, it is primarily because the ants are attached to other food. The stomach of a *Hylophylax naeviodes*, which was accompanying an army ant swarm, contained "spider parts but no ant remains" (Howell, 1957: 93). The stomach of a *Formicarius analis* also contained no ants, but a lizard was found in it. Howell (1957: 92) commented, "As one of the Barecrowned Antbirds had also eaten an *Anolis*, it may be that small lizards form a regular part of the diet of these formicariids." Since it is known that some of the antbirds eat the army ants as well as spiders, lizards and Orthoptera, a more reliable conclusion on the extent that these birds feed on the army ants will have to await a more thorough study of the stomach contents of large series of birds.

The calls of the antbirds mingle with the buzzing of numerous flies and the rustling of dried leaves as spiders, amphipods, cockroaches and other arthropods flee from the advancing ants. During the dry season the flies accompanying the swarm, the fleeing arthropods, and the thousands of ants running on the dried leaves produce a distinctive sound. This is less evident in the rainy season when the forest floor is thoroughly soaked. On one occasion I was first attracted to a swarm raid of <u>burchelli</u> by the sound of hundreds of waterbugs fleeing up the bank from a stream bed. The stream was almost dry, and the bugs had been resting mainly on the ground when the raiding ants drove them up the bank.

A large swarm raid of <u>burchelli</u> will be accompanied by over a thousand flies which hover over the ants or dart from leaf to leaf in the center of the swarm or just in advance of the swarm. These flies have been thought to be parasitic on the ants, but most if not all of them are parasitic on insects flushed out by the ants. (They will be discussed more fully below in the section, Diptera Associated with the Swarm Raids.) These flies, like the antbirds, are not found over the column raids of other species of army ants. The flies can be heard for a distance of five to ten meters, and on several occasions I have found swarms by locating the source of this buzzing. The dipterist, Dr. Charles H. Curran, who undoubtedly was more conscious of the buzzing of flies than the calling of the antbirds, reported (1934a: 1), "In every case in which I located armies of ants I was attracted by the noise of the flies."

Emigrations of Eciton burchelli

The increase in raiding activity that occurs after the siesta period when colonies are in the nomadic phase seems to take place at the same time with *burchelli* and *hamatum*. However, the emigrations of *burchelli* frequently do not start until after 6:00 p.m. which is somewhat later than those of *hamatum*. Some emigrations do not start until after 8:00 or even 10:00 p.m. Even when the emigrations start between 3:00 and 6:00 p.m., the queen does not usually emigrate until after 8:00 p.m. The times when queens were seen along emigrations are given in table 1. The somewhat later appearance of the *burchelli* queens compared with those of *hamatum* is attributed to a combination of the later beginnings of emigrations and the larger sizes of the colonies. It may also be true that the *burchelli* queens emigrate more frequently after about 50% of the workers have left the old bivouac rather than nearer 90%. The earliest that a queen of *burchelli* was seen on an emigration was 7:45 p.m. This case may have been abnormal because I returned the queen to the bivouac at 10:15 a.m. the same day. Since the colonies are much larger than those of *hamatum*, emigrations which start near 7:00 p.m. may not be completed until about 3:00 a.m. the next morning. If there is a heavy rain during the night, an emigration may be prolonged into the daylight hours the next morning.

The emigration columns average about twice the width of those of *hamatum*. Since the swarm raids do not advance more than 75 to 150 meters from the bivouac, as a rule, the mean emigration distance is less for *burchelli*. The greater amount of traffic and the more easily excitable nature of the workers are probably the primary factors contributing to the greater development of ant roadways along *burchelli* emigrations (see figures 5 to 7). Colonies with broods of young larvae have weaker roadways than those with larvae almost ready to spin, and colonies with sexual broods have even larger roadways. The workers seem more highly excited by the larger larvae, and the difficulty in carrying the sexual larvae apparently further increases the ant roadway. Guard workers likewise are more common with *burchelli* and are increased with any disturbance or excitement of the workers.

The retinue of the queen on the emigration may consist of several hundred workers and is always larger than with *hamatum*. This greater mass of workers appears to slow the progress of the queen, and when she moves slowly more workers join the retinue. On the few occasions where a queen was seen emigrating along a smooth log several meters in length, the number of workers accompanying her greatly decreased compared to those with her when she was crossing leaves. If there is considerable disturbance of the column, the number of guard workers will increase until there is a solid row of them along both sides. These solid rows of guards were never seen with any other species of *Eciton*. Light seems to disturb an emigration of *burchelli* more than one of *hamatum*. The greater disturbance may be due more to the greater number of ants along the column rather than to a greater sensitivity of the workers to light. Otherwise the observations mentioned earlier regarding the queen and guard workers along emigrations of *hamatum* apply also to those of *burchelli*.

The same sequence of events also takes place during the emigrations of *burchelli*; however, all stages are more prolonged due to the larger sizes of colonies. I rarely saw the end of an emigration because the last ants usually left the old bivouac after midnight.

Bivouacs of Eciton burchelli

The bivouac of burchelli in addition to their larger size are distinctly "more epigaeic" or more elevated than those of hamatum. Schneirla, Brown and Brown (1954: 279) have shown that burchelli has fewer subterranean and many more elevated bivouacs than hamatum. Bivouacs of burchelli did not touch the ground in 33% of 270 cases, whereas those of hamatum were elevated in only seven per cent of 440 cases. Moreover, when bivouacs of burchelli were elevated, they were usually more than one meter from the ground, whereas those of hamatum were below one meter. A colony of burchelli will apparently bivouac in a sheltered spot at any height in a tree. Using binoculars, I have watched emigrations and raid columns which went up trees to bivouacs at least 20 meters above the ground.

The bivouacs of burchelli shift by small amounts during the statary period even when they are well enclosed and not disturbed. Although statary bivouacs were not observed every day, three colonies are known to have shifted their bivouacs from five to more than 55 cm. at least several times throughout that phase. Possibly these shifts were primarily due to the subtraction and addition of workers resulting from raiding, but at least some shifting occurred in the absence of a raid. An additional colony, '55 B-IV, which had a brood of male and female cocoons during the statary phase shifted as shown in figure 66. This shifting may have been influenced by the presence of the sexual brood which was kept in the section of the bivouac away from the old queen. This bipolarity may normally result in some lengthening of the bivouac.

Refuse Deposits of Eciton burchelli

Eciton burchelli is the only species of army ant included in this report which has extensive epigaeic refuse deposits. As a direct consequence of its feeding on a variety of adult arthropods, there is a considerable amount of refuse from the more sclerotized parts of the prey. This refuse, empty cocoons and dead workers are put by the ants in more or less distinct areas which I have termed refuse deposits. Short columns extending out from the bivouac are here called "refuse columns" whether or not they go to distinct refuse deposits. Many ants seen along these columns were not carrying any refuse but appeared to be just wandering back and forth from the bivouac. The workers defecate along the columns as well as in the refuse deposits, and the fecal material may form a distinct white trail during the statary phase.

Typical arrangements of these deposits are shown in figures 65 to 68, and figure 13 is a photograph of part of one refuse deposit. These refuse deposits or kitchen middens were invariably found on downward slopes away from the bivouac. Almost no refuse was found directly under the bivouac or within 20 cm. of the edge of the nest. The columns occasionally extended more than one meter from the nest; but in these cases, the bivouac was located in a tree, or the slope down to the refuse deposit was steep. These refuse columns and deposits have been largely ignored in the literature about the army ants. Moreover, the arthropods found in refuse deposits are mostly different from those found in bivouacs. Some of these arthropods probably are restricted to the refuse deposits or at least are more frequently found in them than in any other ecological niche. A more complete description of these areas and information on the arthropods associated with them will be given below in the section, Refuse Deposits of Army Ants and the Arthropods Found in Them.

Because workers of burchelli emerge over a period of at least six days, their empty cocoons can be found in the refuse deposits from one day before the last statary day to the fourth nomadic day. Empty cocoons are most abundant on the first nomadic day, and on the second nomadic day they are much more abundant than with hamatum colonies on that day. The number of cocoons on the second nomadic day may give the area around the bivouac the appearance of a statary site, except that much less booty refuse is found, and the site would usually be less enclosed or sheltered.

Size of Colonies and Broods of Eciton burchelli

Schneirla gives fewer estimates of the sizes of colonies of burchelli than for hamatum; but these estimates, like those of hamatum colonies, have been increased in his later papers. An early estimate for a "very large" colony was "more than 200,000" (Schneirla, 1949b: 37), and his largest estimate is 300,000 to 1,500,000 workers (Schneirla, 1957b). I estimate 150,000 to 300,000 workers are in the smallest colonies after a colony division.

Three and one-half quarts of preserved workers and worker-producing larvae taken on the 14th nomadic day from colony '55 B-IV-N were completely counted and found to contain about 77,800 workers (including 1,600 majors) and 104,800 larvae. This sample was taken about 11:30 a.m. when many workers were on a backtracking column resulting from removing the queen from the emigration column on the preceding night. Probably less than one half of the workers were taken. On this basis the colony consisted of 180,000 to 250,000 workers. This colony was at the end of the first nomadic phase after a colony division, and it was one of the smallest if not the smallest colony of *burchelli* which I have ever seen. Many *hamatum* colonies are of equivalent size. Probably about 90% of the larval brood was taken, indicating a total brood of 116,000 for this daughter colony. The brood total probably is accurate to within 20,000 larvae.

The second daughter colony, '55 B-IV-S, was considered to be about twice as large as '55 B-IV-N. (According to T.C.S. proportions were 40:60, letter of Dec. 3, 1961) A sample of four quarts of preserved workers and larvae were taken from this colony, but this was clearly less than one half of that daughter colony. This sample must include about 100,000 workers and 150,000 larvae. On the basis of the relative sizes of the two daughter colonies, '55-IV-S probably had approximately 500,000 workers. The parent colony would thus have had about 700,000 workers and brood of 250,000 to possibly 350,000 full-grown larvae. This astonishing brood was laid by the single queen of the parent colony. Estimates of brood size published by Schneirla are lower than these but have been increased from "25,000 or more" (1949b: 37), to "60,000 or more" (1956a: 2), to "120,000+" (1957b: 266).

Estimates based on samples from other colonies are comparable but less accurate than the ones given above for the '55 B-IV colonies since smaller proportions of the colonies were taken. Samples of 100 ml. of tightly packed ants of approximately the normal size distribution and not including brood, range from about 4,000 to 6,000 workers. These figures are essentially the same as for *hamatum*. However, each of these samples was less than 1/100 of a large *burchelli* colony.

Estimates based on emigration rates are somewhat lower than the above and start at 300,000 workers for colonies of medium size. Unfortunately, the maximum rate of emigration in ants per second could not be determined accurately. Maximum emigration times are not known, but some colonies must have over 500,000 workers based on estimated emigration rates and durations of over eight hours.

The total egg production for a *burchelli* queen would be between 55,616 and 66,100 eggs if based on counts of ovarioles and oöcytes determined by Hagan (1954a, 1954c). Although the estimate of the number of ovarioles might be inaccurate, one would expect that the discrepancy between Hagan's estimate for an entire brood and my counts of larvae lies primarily in the oöcyte count. Possibly the eggs develop at such a fast rate that the first eggs have been laid before the last eggs to be laid can be distinguished in the ovarioles.

Since a large percentage of an egg brood of *burchelli* has never been counted, there is no evidence that a reduction in the size of a worker brood during the nomadic phase occurs, but perhaps the workers normally eat part of the eggs or larvae of a worker brood.

Sexual Broods and Colony Division of Eciton burchelli

Colonies of *E. burchelli*, like those of *hamatum*, may have a brood consisting solely of males and queens during the dry season. Observations on these broods and several subsequent colony divisions have been published by Schneirla (1948, 1956a) and Schneirla and Brown (1952). It was considered "quite possible" that colonies of *burchelli* have sexual broods earlier than *hamatum* (Schneirla, 1948: 91). Subsequent observations did not show as clear a separation of almost a month in the timing of these broods (Schneirla and Brown, 1952: 10). However, a tendency for burchelli to have males earlier is still indicated and is further supported by observations made during 1956.

Eleven adult males were taken between 17 March and 11 May 1956, compared with 11 for hamatum taken between 9 May and 4 July 1956. The males were taken on the following dates, and unless other data are given the males were all alates taken at lights in the laboratory clearing: 17 March (1 dealate from emigration column of colony E-132), 17 April (1), 19 April (1), 19 April (1 flew to light between 12:30 and 2:00 a.m.), 19 April (3 seen in the bivouac and 1 taken from emigration column of colony E-149, 1 dealate from emigration column of colony E-148), 28 April (1 dealate from emigration column of colony E-152), 10 May (1 taken at 8:30 p.m.), 11 May (3 taken at 8:30 p.m.).

Although worker broods appear to be considerably larger in colonies of burchelli than in those of hamatum, the numbers of males and queens produced by both species are nearly the same.

The oldest known burchelli queen was recovered after four years and two months, and she probably lived at least five years. Dr. Schneirla marked this queen, and I returned her to her colony, '52 B-IX, on 10 March 1952 on the second nomadic day when her gaster measured 11.9 mm. in length. When the same queen was found on 12 May 1956 in colony E-148 also on the second nomadic day, her gaster measured 14.0 to 14.5 mm. The later measurement was made at 3:45 a.m. shortly after the first nomadic emigration had been completed. In order to determine whether complete contraction of the gaster had occurred, the queen was again brought to the laboratory on the sixth nomadic day. At this time the gaster was the same length, and thus two to three millimeters longer than measurements of other queens in the middle of the nomadic phase made by Schneirla (1957a: 119). These measurements suggest that as the queens get older their gasters contract less during the nomadic phase so that they may appear continually physogastric. Before the work by Schneirla it was generally assumed that contracted queens were young and physogastric queens mature or old. Schneirla (1944c; 1958: 218-219) has shown that the age of the queen is not the primary factor in the changes observed in the size of the gaster. The record for the queen of colony '52 B-IX indicates that "physogastric" queens should be observed to determine whether they are actually laying eggs.

A dealate male was taken on 17 March 1956 from an emigration column of colony E-132 at 8:11 p.m. more than 30 meters from the old bivouac. No other males were found in the emigration column of E-132 which was watched continuously from 8:00 to 9:25 p.m. However, on the previous night between 6:30 and 6:40 p.m. one male (or possibly two) was seen five meters above the ground on the trunk of the tree in which the statary bivouac was located. The male was seemingly trying to join the raid column on which ants were returning to the bivouac located more than 12 meters up the tree. Twice the male flew away from the column but returned to it about a half meter away. Workers could be seen congregating around the male, but its ultimate fate could not be determined because of the height. This male did not come from colony E-132 which had a brood of callow workers. If colony E-132 had a sexual brood in the preceding nomadic phase, the adult males would have emerged about 12 February. The earliest record for alates of burchelli on Barro Colorado Island appears to be 28 February 1946 (Schneirla, 1948: 93).

In addition, males probably never remain in the colony in which they are produced at the end of the statary phase following their emergence (*l. c.*).

On the same first nomadic emigration on which the dealate male was taken, the queen was taken at 9:25 p.m. Her gaster was clearly somewhat swollen and when the queen was etherized on the following morning her gaster was still 11.9 to 12.0 mm. long. This is near the average for queens on the second nomadic day (Schneirla, 1957a: 119). This queen must have laid the current and previous worker broods. Unless she developed with a sexual brood at an atypical time of year, she probably was at least one year old when taken from the emigration column. She did not have a greatly swollen gaster which might be expected if she were more than three years old if the case for the queen of colony '52 B-IX is typical. Thus, the queen of colony E-132 was not a virgin and was probably between one and three years old.

On the morning of 18 March after queen E-132 had recovered from ether and was walking around in a petri dish, the dealate male found in the emigration column was added to the dish. Copulation started within one minute and the pair remained together from 10:15 to 11:17 a.m. For the first 15 to 25 minutes the male constantly moved his antennae and front legs in large arcs. Only occasionally did it look like he was stroking the queen. The male held the queen by his middle and hind legs, never with his front legs. He also grasped her petiole behind the horns with his mandibles. At no time did he hold onto the horns themselves. The queen walked around a little during the copulation but was never very active. At times the pair tended to fall over on one side, and after photographs had been taken at several angles, the male was pushed completely to one side to get a better view of the end of the queen's gaster. The turning of the dish, the taking of more than a dozen electronic flash photographs, and the tipping of the male may have shortened the copulation time. After being coupled continously for an hour and two minutes, the pair separated. The male was unable to walk and was immediately preserved. The queen walked around in the dish but was not as active as other queens kept in the laboratory for an equal amount of time. She was returned to her colony and later was seen in an emigration. It is clear from the above evidence that a queen sometimes mates more than once and may mate annually.

Activity Cycle of Eciton burchelli

The major features of the activity cycle of burchelli are identical to those for hamatum as shown in figure 63. However, more variability occurs in the length of the nomadic phase in burchelli. This phase can last from 11 to 17 days compared with 16 to 18 days for hamatum when colonies have larval worker broods. In contrast the statary phase shows slightly less variability, varying from 19 to 22 days, whereas it ranged from 18 to 22 days in hamatum (Schneirla, 1957a: 107). In the dry season the nomadic phase may be slightly longer than in the rainy season, but too few entire nomadic phases have been followed to make this conclusive. When a colony has a sexual brood, the nomadic phase may be decreased to nine or ten days (Schneirla and Brown, 1950: 322).[1] The

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[1] Unfortunately, the lengths of the three nomadic phases observed by Schneirla for colony '46 B-I were incorrectly given as 10, 10 and 8 days by Schneirla and Brown (1952: 17). They should have been given as

statary phase is the same length when a colony has a sexual brood. (Colony '48 B-XVII /Schneirla and Brown, 1950: 306-307/ had a statary phase of 25 days, but this colony did not emigrate until "all or virtually all" the males had emerged, whereas other colonies had males still in cocoons on the first nomadic emigration. Frequent sampling and other disturbance of the colony, especially the removal of two queen cocoons, possibly affected the length of the statary phase.)

The statary phase does not start until after the larvae have been spinning for several days. Although hamatum larvae spun cocoons almost exclusively on the first and second statary days, those of burchelli spun on the last three nomadic days and at least the first three statary days. The proportion of the brood which is enclosed on any of these days is not known.

Although the initiation of the nomadic phase is attributed to the stimulation of the older workers by the callows, it is interesting that sometimes the first nomadic emigration occurs before one half of the callows has emerged. The callows were not seen to take part in the raids of the first and second day. However, at least 50 callows were

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12, 13 and 10 days as one can determine from the data published by Schneirla (1949b: 30-32). The last figure in each group is for the length of the nomadic phase when the colony had a sexual brood. These corrections would also raise the total development times given in the table published in 1952 to 42, 44 and 41 days. These corrected total development times are still two to five days less than the total development times for hamatum. Perhaps a shorter total time of development does not always occur in burchelli, judging from two records of nomadic phases of 17 days reported by Schneirla (1957a: 107).

seen carrying unopened cocoons on the first nomadic emigration of colony E-110. This colony emigrated when about 40 per cent of the callows had emerged and some major workers were still in cocoons.

Raids appear to get larger toward the end of the nomadic phase, but no quantitative evidence can be given to support this. Although no clear trend is evident in the lengths of emigrations throughout the activity cycle, there may be a tendency for colonies not to emigrate for one night near both the beginning and end of the nomadic phase.

Interrelations Among Individuals of Eciton burchelli

All the observations reported above in the section on interrelations among individuals of *E. hamatum* apply also to *burchelli*. An additional observation on the longevity of queens in the laboratory was made for *burchelli*. The queen of colony E-136 taken on 28 April 1956 at 9:10 p.m. was only weakly twitching on 1 May at 9:00 a.m. and therefore lived only two and one-half days in the laboratory.

The workers seem to be more attracted to the posterior margin of the first tergum of the queen than to any other segment. Perhaps glands for a "queen substance" are located here, but Hagan (1954b) did not report finding any hypodermal gland cells in the gaster of the queens of *burchelli*.

The workers were seen to carry larvae out of the bivouac to spinning clusters both during the day and night. At night there seemed to be slightly less traffic by the workers, but the size of the cluster and the number of larvae in it seemed to be the same. Colony E-156, when visited between 2:00 and 3:15 a.m. on the third statary day, had a column one to three ants wide and a second column three to five ants wide continually present between the bivouac and the spinning area. Less than ten per cent of the ants in these columns carried larvae or cocoons. These columns and the spinning areas were distinct from the refuse columns and deposits.

Eciton vagans (Olivier)

Borgmeier (1955) has divided Eciton vagans into seven subspecies on the basis of differences found among males and queens. However, he could not find subspecific differences among the workers. Almost all the observations on the behavior of vagans have been made on the subspecies mutatum, found on Barro Colorado Island, or angustatum, found in México. The ranges of these two subspecies overlap in Costa Rica according to Borgmeier.

Throughout its range E. vagans appears to be much more rarely seen than hamatum and burchelli, although the number of colonies of each species may be approximately the same. A total of 13 colonies of this species was found on Barro Colorado Island during 1956, compared with 18 of burchelli and 32 of hamatum. The lower number of colonies of vagans probably can be more reliably attributed to the time and method of its raiding and emigrating rather than to a smaller number of colonies. These differences will be discussed below.

Although workers of vagans are slightly larger than those of hamatum and burchelli, they have a weaker bite. Moreover, when several dozen workers were running on my legs or uncovered hands, not one tried to sting.

Fragmentary evidence given below and that reported by Schneirla (1947: 5, 9) shows that vagans has synchronous broods and probably has alternating nomadic and statary phases. There is no evidence to indicate how frequently this species may emigrate or how long the nomadic phase may be. The only evidence regarding the possible length of a statary phase is that based on the length of time that a worker brood kept in the laboratory remained in cocoons. This sample was taken from a bivouac of colony E-154 on 30 April 1956 when the brood was partially enclosed in newly spun cocoons. The previous day this colony was in the identical spot, but the brood seen consisted of unenclosed larvae. The first major worker emerged in the laboratory on 22 May which would indicate a statary phase of 24 days, if 29 April was the first day of that phase. Unfortunately it is not known how long the colony remained in the site where the sample had been taken. Moreover, samples of brood may develop at a slower rate or the adults may emerge later than those remaining with the colony in the forest judging from a case when *hamatum* cocoons were kept in a laboratory nest. Since all broods of *vagans* which have been observed are synchronous, one would expect that *vagans* has statary and nomadic phases similar in length and regularity to those of *hamatum*.

Like all other ecitonine queens, those of *vagans* are short-lived in laboratory nests. The queen from colony E-212 was clearly dying at 9:00 a.m. on 12 July after almost three days in the laboratory. However, the workers with this queen also were either dead or dying. The death of the queen may have been hastened by a macrochelid mite which was feeding on a small amount of liquid along the posterior margin of the first gastral segment. The mouthparts of the mite were not inserted into the membrane between the terga, but this mite may have punctured the membrane earlier. No similar fluid nor macrochelid mite has been seen on any other ecitonine queen.

Raids of Eciton vagans

Eciton vagans feeds primarily on ants judging from the booty seen in raid columns. Adult ponerines were among the booty, and more adult ants may be killed by vagans than by hamatum. Other adult insects are attacked, but no raid columns were seen to go up any vegetation more than a few centimeters above the ground. However, Fiebrig (1907a: 84) reported that E. vagans (det. Forel) raided a Polistes nest under the eaves of a house. He also reported that they attacked bees which possessed stings (t. c., p. 87) [the exact insect was not named, but perhaps the honeybee or a wasp was the species attacked]. A click beetle (Elateridae) which fell among some workers milling around a hole near a bivouac was immediately attacked. The number of ants attacking this beetle increased to about 50, and they bit, pulled and attempted to sting it for 40 minutes. The ants were then removed from the beetle and preserved. The beetle had lost four segments of one antenna, ten segments of the other, and all tarsal segments were injured or had been removed. Both hind tibiae were also partially pulled from their sockets. When the beetle attempted to walk, it could hold only one leg in a normal position; all the others stuck out at odd angles and were quite useless. As far as I could determine, the ants never were successful at stinging the beetle although they tried to sting repeatedly. The elaterid repeatedly clicked while it was being attacked and while I was examining it. Perhaps this clicking helped to increase the number of ants attacking the beetle. If the beetle had not been collected, it probably would not have been killed but would have lost most of its appendages, since other species of army ants were seen to desert similarly maimed beetles.

The raids of vagans resemble those of hamatum except that the columns start from subterranean bivouacs and extend only 10 to more than 100 meters along the surface of the ground. In most cases it was impossible to tell whether the bivouac was near the hole into which the ants disappeared. Schneirla (1934: 317) reported that the "consolidation columns that connect the raiding front with the bivouac mainly follow a subterranean course, the advanced part of the raid forms on the surface a system of branches and anastomosing columns.... If little booty is taken, the ants withdraw along their principal trail into the ground, and may soon emerge at a point some meters removed to repeat the process there." Although this extension of a subterranean system undoubtedly occurs to some extent when vagans raids, there was little direct evidence for it during my observations. Two colonies had raid columns which entered holes at two or more points along their extent. However, six or more colonies had raid columns extending along the surface of the ground for at least 25 meters and more than 100 meters in three cases. These started from bivouacs, and the ants did not shift to a subterranean route even though they were capturing no prey within 25 meters of the bivouac and were raiding during daylight.

No raid columns were seen between noon and 6:00 p.m., but some raiding must occur during that period since columns were seen at 11:50 a.m. About three fourths of the raiding observed occurred between 6:00 p.m. and midnight. Presumably raiding is frequent between midnight and 8:00 a.m., but observations were not as frequent during those hours. Only four colonies were found raiding between 9:00 a.m. and noon even though more time was spent searching in the forest during those hours than during any other period of three hours. Probably most raids start between 6:00 p.m. and 6:00 a.m.

On one occasion a small swarm raid of vagans was discovered at 10:50 a.m. The ants covered the ground as extensively as a swarm raid of burchelli. Accompanying the advancing swarm were several of the same species of Tachinidae which are found over swarms of burchelli. However, by 11:20 a.m. the swarm front had narrowed to a strong, forked raid column. The bivouac was found only three meters from the spot where the swarm front was discovered at 10:50 a.m. A brood of almost full-grown reproductive larvae was found in the bivouac. A swarm raid clearly is not typical behavior for vagans, and this unusual swarm is probably attributable to increased excitement due to the sexual brood and the fact that the raid was observed close to the bivouac. Other observations indicate that raids of vagans usually do not start this late in the morning.

Emigrations of Eciton vagans

The times when emigrations of vagans start probably are more variable than those of hamatum and burchelli. Only three emigrations of vagans were observed during 1956, and these had started some time before they were discovered. The earliest one observed was an emigration of colony E-180 found on 31 May 1956 at 8:15 p.m. At this time much brood was being carried, at 8:50 p.m. the queen was taken, and at about 10:20 p.m. the last ants passed. The exact locations of either bivouac were unknown, but the observations were at least 15 meters from the old bivouac. This emigration may have begun on the previous night. However, on the night it was observed it probably started before 7:00 p.m.

and may have started before 6:00 p.m. A backtracking column was seen along the emigration route about 24 hours after the queen was taken, but it is not known when this column was started.

When colony E-240 was discovered on 7 August 1956 at 8:15 p.m., it was emigrating with a brood of alate males. The column was immediately followed toward the new bivouac, but after about 50 meters the column became thin, and it was not followed further. Probably the emigration had started about 7:00 p.m. From 8:15 to 10:50 p.m. the emigration was watched intermittently, and the queen most likely emigrated during that period, although she was not seen. At 10:50 p.m. the column had decreased to a width of one or two workers, and no males were in it. Further details about this emigration are given below in the section on sexual broods.

A third emigration observed was that of colony E-219 discovered on 24 July 1956 at 2:30 a.m. This column followed the emigration route used 20 days earlier by colony E-204, *E. dulcius*, for several meters along the *edge* of a concrete sidewalk. However, in places on the surface of the sidewalk as well as across dirt and a lawn, colony E-219 deviated from the route of the *dulcius* colony. The queen of colony E-219 was taken at 3:03 a.m., and the number of workers gradually decreased following the queen. Over 90% of the ants must have emigrated before the queen left the old bivouac, assuming her progress was not impeded. The end of the emigration column, like such a column of *hamatum*, had many ants running for distances of about 30 cm. toward the old bivouac and then turning and following the rest of the colony. One stray worker passed at 3:46 a.m. more than five meters behind the last ants. However, at 3:49 a.m. several backtracking workers came from the direction of the new bivouac. It is not known whether a steady backtracking column was started at that time, but this would appear to be exceptionally soon for a backtracking column. No observations were made during the day after the queen was taken, but on the following morning, 26 July, the backtracking column was still present but decreased between 7:00 and 8:00 a.m. It did not start again until about 4:00 p.m. About 7:00 p.m. an attempt was made to trap workers by placing a small laboratory nest with the colony's queen and a few workers in the center of the backtracking column. This nest was about 20 cm. square and 2.5 cm. high with a glass cover and two entrance tubes large enough for the major workers. Although the tubes were placed in the column for about an hour and vagans and other species of Eciton had previously run through the tubing, none of the workers entered the nest. When the glass cover was removed, no workers entered the nest chamber after an additional hour, and the queen was then placed in the backtracking column. She promptly moved toward the new bivouac. The promptness with which this queen and other Eciton queens moved toward the current bivouac suggests that either the trail is polarized or the ants have some other method for determining the direction toward the bivouac.

The retinue of workers accompanying the queen of colony E-180 was quite large and similar to an average retinue with a hamatum queen. There were some guard workers along the margins of the column, but these usually left their positions in a short time, and no continuous rows of guard workers were present at any time. The guard workers were always dark or old workers, even though numerous callows were in the emigration column, and about the same number of callows as dark workers were carrying larvae. No callow workers were seen being carried. This colony probably was in the middle of the nomadic phase judging from the size of the worker larvae.

The retinue with the queen E-219 had a small number of majors which were clearly more excited than majors which were running in other parts of the emigration. However, although the majors ran back and forth, spread their mandibles, and rapidly vibrated their antennae, they did not rear up with their front legs off the ground. Two intermediate workers were partly running and partly clinging to the gaster of the queen with their heads over her gaster. When the queen was removed, the retinue continued along the emigration without her with only a slight disturbance noticed. The retinue was not followed.

Since eggs were being carried, the emigration of colony E-219 was observed probably on or near the second nomadic day. Nevertheless, a few callow workers were carrying booty or army ant larvae, and only a few callows were being carried by dark workers.

The emigrations of *vagans* had no ant roadways except for the emigration with the alate males discussed below under sexual broods. Since *vagans* columns seldom left the ground and did not even travel on logs as much as *hamatum*, flanges of ants were not apt to be seen. Only a single small flange was seen when a colony had a worker brood. The emigration of colony E-180 travelled for about one meter across leaves of wild pineapple plants, and a small flange of workers was seen on one of the smooth leaves. This flange was continuously present for more than one hour before the queen was seen in the column.

Bivouacs and Refuse Deposits of Eciton vagans

On Barro Colorado Island only subterranean or well-sheltered bivouacs of *E. vagans* have been found; however, "more exposed bivouacs... were observed under other conditions in Southern Mexico (Schneirla, 1947)" (Schneirla, Brown and Brown, 1954: 279). In the paper published in 1947 (p. 5, 9), the two colonies of *vagans* discussed, colonies "J" and "X2," had bivouacs inside rotten logs or partially in debris under the logs. The majority of ants in both cases were apparently not in a large cavity but distributed throughout many small cracks and passages within the rotten wood. Neither of these cases should be considered as "exposed" in the sense of Schneirla, Brown and Brown (1954: 278-279).

Fiebrig reported that on at least several occasions *E. vagans* was found bivouacking in the subterranean nest of *Atta sexdens* or *Atta* sp., but it was thought that the army ants occupied only the more peripheral and less-used sections of the nests. The two ant species were not seen together, and it was not known whether the army ants killed the leaf cutters (Fiebrig, 1907a: 86; 1907b: 154-155).

All the bivouacs of *vagans* which were located during 1956 were sheltered on all sides and were primarily underground. Although none was completely dug out, partial descriptions of these nests will be given since few nests have been reported. Colony E-154 was first traced to the bivouac on 29 April by following a thin raid column at 6:15 p.m. The ants disappeared under leaves, and when these were brushed away, the entrance to the bivouac was indicated by about a dozen phorids which were hovering over the hole in the ground. When the ground was vibrated by cutting a small liana, several hundred workers including many carrying larvae ran out of the hole. Dark workers and some rather dark callows pulled small leaves and pieces of leaves and dirt into the entrance hole almost blocking it completely. There was a noticeable air current on the slope of the hill, and this current or my weak headlight may have caused the workers to decrease the size of the hole. At 8:15 a.m. the following morning 5,000 to 10,000 workers were clustered on small roots running through a cavity 25 to 30 cm. in diameter. The origin of the cavity is unknown, but the absence of loose dirt in cracks around the cavity or on the surface of the ground suggests that it was not made by the army ants. The top of this cavity was almost 30 cm. below the surface of the ground. At a depth of 50 cm. at least four principal passageways continued downward to an unknown depth. A total of 2,375 workers plus 59 majors and 302 worker larvae and cocoons were taken. Probably these larvae had been brought to or near the surface of the ground for spinning while most of the brood and adults were considerably deeper in the ground. Many of the larvae taken were enclosed in thin, incomplete cocoons. No queen nor males were found. While I was digging up the colony, the odor of the ants increased considerably; but no flies other than the few phorids were seen near the hole.

Another bivouac was found on 9 July by tracing the small raid swarm and column of colony E-212 discussed earlier. A diagram of this bivouac as it would appear if viewed directly from above is given in figure 64. This is the only time a larval sexual brood has been found in a bivouac of this species. A large number of leaves and small branches covered the area of the bivouac, but these are not indicated in figure 64. The only large cluster of ants was hanging from a log about 15 cm. in diameter, from a small branch, and from the side of the large rock. This mass was completely covered by other small branches and leaves. No callows were among the ants comprising the outer layer of this cluster though there were some in the center. There were a few sexual larvae scattered throughout this cluster. Callow workers were primarily in distinct groups between leaves and on the ground under leaves. Some were along the south and southeast edges of the rock where there was a pile of loose dirt mixed with scattered refuse from booty. The booty refuse was so dispersed that it was impossible to get a sample of it without including considerable dirt. A few dark workers were seen carrying out dirt from under the rock and depositing it on this pile. No myrmecocoles were conspicuous near the refuse or nest before the bivouac was disturbed. Some ants were also going under the rock along the north side where a little digging apparently had been done by the army ants. A large proportion of the colony may have been underground. The rock could not be moved, but attempts to push sticks underneath indicated that there was no large adjacent cavity.

Directly on top of the rock and throughout the stippled area north and east of the rock there was a layer of leaves and twigs. Under and among these were many workers which were fairly evenly distributed except for two distinct clusters consisting solely of callows and a third cluster of excited workers in which the queen was found. The clusters of callows had no older dark workers mixed with them, and these clusters did not rapidly disperse when disturbed like many of the darker adults, but remained together and appeared lethargic. In contrast, the cluster containing the queen had only a few callows but numerous dark workers including a noticeably greater number of majors than any of the other clusters. Many dark workers were running near the queen cluster, with some joining the cluster. Others left the cluster so that its size remained about the same. In addition, the majors were highly excited like those with queens of other species of Eciton. No tight mass of minor workers was found around the queen. It is possible that the queen moved a short distance as soon as I had disturbed the colony. However, it is quite certain that she was not on top of or under the rock. She may have been in the large hanging cluster or else on the ground nearer to the hanging cluster.

A brood of sexual larvae about three-fourths-grown was quite uniformly scattered on top of the rock and on the ground near the north and northeast sides. A few were in the hanging cluster. About two thirds of the larvae had no distinct groups of workers with them. Each larva of the remaining third was surrounded by a small cluster of up to 20 workers, some of which were clinging tightly to the larva. The larvae surrounded by clusters of workers were not concentrated in any one part of the bivouac. A total of 79 larvae was taken, which must have been at least half of those seen. Three or four larvae were partially shriveled at the time the bivouac was uncovered, indicating that the workers had been feeding on them. All the larvae taken are males; however, the small number of larvae and adults seen indicates that a large proportion of the bivouac , including probably a few queen-producing larvae, was underground. A small amount of booty was dispersed among the ants and not concentrated near the larvae.

Although a raid was in progress, it probably had started about 10:30 a.m., only about one hour before the bivouac was found. A small, steady amount of booty was being brought to the bivouac. A large percentage of the colony could not have been participating in the raid at this time. These raiding ants probably came primarily from the hanging cluster and may have filled in shallow cavities under the north and northeast edges of the rock when the entire colony was at the bivouac. Approximately 10,000 workers plus 240 majors were taken from the bivouac. Over 50% of those seen must have escaped. Two samples of 100 ml. of ants included 2,258 and 2,837 workers (including majors). Since similar counts of <u>hamatum</u> and <u>burchelli</u> ranged from 3,000 to 6,000, these low counts reflect the larger size of the <u>vagans</u> workers and the higher proportion of majors. (An attempt was made to collect as many majors as possible, and the high proportion of majors, 1:40 intermediates, is not typical for this species.) Judging from the incomplete bivouacs and emigrations seen, colonies of <u>vagans</u> are probably smaller than those of <u>hamatum</u>.

Colony E-240 emigrated to a subterranean bivouac under a large palm with many stilt roots where digging was not practical. Workers were seen carrying dirt and wood detritus to small piles between the stilt roots, but the source of this material was not discovered. No booty refuse was seen in these piles. The night following this colony's emigration to this site, there was no emigration up until 8:05 p.m., and no observations were made after that time.

Sexual Broods of Eciton vagans

One colony of <u>Eciton</u> <u>vagans</u> was found with a sexual brood of larvae almost full-grown, and another colony was found with a brood of recently emerged alate males. The latter colony, E-240, was found emigrating on probably the second nomadic day following a colony division. A brood of eggs and young larvae was being carried, but only two eggs and two larvae were preserved. This emigration came out of a large brush heap and vine tangle in which the bivouac or at least the start of the epigaeic emigration column was located.

The workers were more excited than those seen on the two emigrations when sexual broods were not present. There were some places where a slight ant roadway, including bridges and flanges of workers, had been formed. However, these were not as well developed as those of <u>hamatum</u> colonies with comparable broods of alate males. Attempts to collect as many males as possible added to the excitement of the workers since a few ants would usually drop off when the males were picked up. My collecting caused the formation of some small clusters of workers surrounding males along the emigrating route. These were similar to the clusters formed when a queen was stopped along an emigration. At least 50 of these clusters were formed, and some of them lasted more than 30 minutes. Almost every male in the column had at least one worker riding on him, or the worker was running along with its legs straddling the gaster of the male. At times as many as seven workers were seen on a male. A new genus of Histeridae, one thysanuran nymph (probably <u>Trichatelura</u> <u>manni</u> Caudell), and many small Limulodidae were seen riding on the males. Each male had a small group or retinue of up to 100 workers accompanying it. These workers were present partly because of the mechanical blocking of the emigration column rather than solely because of attraction to the males.

Along the emigration column it was impossible to tell whether the workers were only riding on the males and possibly licking them as they ran along, or whether the workers were actually clinging to the males by their mandibles. In the laboratory nests the workers continued to follow the males and were clearly seen to grasp the males with their mandibles.

At times they bit the wings firmly enough to fold them. The workers also rode on the wings without grasping them with their mandibles.

The workers not only clung to the males but also licked the gasters and sometimes other parts of the males. A large amount of fecal material (?) from the males was deposited in the vials in which they had been brought to the laboratory. Some of the gasters became completely coated with this white fluid, and the amount of fecal material probably indicates that these males had recently emerged. The workers cleaned some of this material off the bodies of the males but also licked males which had no noticeable fecal material on them.

The fact that no males attempted to fly was an additional indication that the males had recently emerged. None of the males even attempted to spread his wings in the column whether or not workers were riding or clinging to him. After the workers had been removed from them and the males were dropped more than a meter, they still did not move their wings.

Although lights were watched at the laboratory for ten more days after these males were seen, no males of *vagans* were taken at the lights. Colony E-240 was located between 1,200 and 1,500 meters from the laboratory which may be farther than many of the males would fly. The males in the emigration were much more affected by my light than the workers. Although these males invariably turned away from the beam of light, presumably they would become photopositive within a few days. Schneirla (1948: 106) reported that *Eciton* /apparently *hamatum* and *burchelli*/ males withdrew from "very bright lights." My flashlight beam had a much lower intensity than the lights which attracted *Eciton* and other male army ants at the laboratory. The males must become photopositive, either several days following emergence or only after they have started flying.

Most of the numerous males of vagans listed by Borgmeier (1955: 239-246) were probably taken at lights although this was not stated with any of the records.

The bivouac to which colony E-240 emigrated on 7 August was under a large palm tree where digging was not feasible. No ant clusters could be seen. On the opposite side of the tree from the emigration column a raid column extended and booty was being brought to this bivouac during the emigration. On the following night, 8 August, colony E-240 had raid columns at 7:05, 8:30 and 11:10 p.m., but there was no emigration. No males were seen among the ants milling around on the ground at the bivouac site, and there were no clusters of workers.

About 130 males were taken from colony E-240, and the total number of males was estimated at a minimum of between 300 and 500. The colony seemed to be small and may have been a daughter colony. If this number of males was half of the brood, the resulting estimate of a total brood of 600 to 1,000 is comparable to some counts of male broods of hamatum.

Since only 100 to 180 sexual brood larvae were seen in the bivouac of colony E-212, at least two thirds of the larvae were probably in a subterranean part of the bivouac which was not seen. Schneirla (1956a: 4-6) reported that colonies of E. hamatum are strongly bipolar with the old queen in one half of the bivouac and the sexual brood in the other half. In this regard it is interesting that the bivouac of colony E-212 did not show any clear separation of this type. Even if the queen had been in the hanging cluster before the bivouac was disturbed, in that cluster as well as throughout the area where the queen was found, there were scattered sexual larvae. Perhaps the queen larvae were in the subterranean part of the bivouac farthest from the adult queen. The cannibalism of several larvae that was occurring at the time the bivouac was discovered may indicate friction between the old queen or the workers associated with her and the brood.

Eciton dulcius Forel

Eciton dulcius dulcius Forel has been found only in Brasil and Argentina, and the other subspecies, *crassinode* Borgmeier, has been found only on Barro Colorado Island (Borgmeier, 1955: 203-209). The wide geographical area between these two subspecies suggests that they may be two distinct species rather than subspecies. All three castes of *dulcius s. str.* are known, but the male of *crassinode* has not yet been found or associated with the workers. In the forest *dulcius* is most easily confused with *vagans*, but the former lacks a spine on each posterior lateral angle of the head. No striking differences were noted between the behavior of these two species. Although the bites and stings seemed to be more severe than those of *hamatum*, the workers of *dulcius crassinode* did not bite nor sting as readily as either *hamatum* or *burchelli*.

Only eight colonies of *E. dulcius crassinode* were found on Barro Colorado Island, indicating that this species is the least common (or least commonly seen) of the five species of *Eciton* workers studied at that locality. *E. dulcius* has synchronous broods and has been seen emigrating with brood in the larval stage. A colony of *dulcius dulcius* which emigrated with cocoons containing males more than a week before their emergence probably was forced to emigrate since the subterranean bivouac of this colony had been dug up earlier the same day (Bruch, 1934b: 261-263). Numerous light callows were seen on two of four emigrations of different colonies in Panamá, and one of these colonies had a brood of eggs and young larvae at the same time. Presumably the species has a nomadic-statary cycle, but the frequency of emigrations and the lengths of the phases are unknown.

Raids of Eciton dulcius

Judging from the booty being carried in columns, the most frequent prey of *Eciton dulcius* were Formicidae. Ponerinae were apparently captured more than any other subfamily of ants, and even *Paraponera clavata* (Fabricius) was killed. In Brasil Borgmeier (1955: 208) also saw *dulcius s. str.* carrying pupae of Myrmecinae and larvae and workers of *Dinoponera australis nigricolor* Borgmeier. Although *dulcius crassinode* was never seen to raid any wasps or other insects in trees, shrubs or on buildings, it would readily eat *Polistes* larvae and callow adults removed from capped cells and placed in laboratory nests. Bruch (1923: 173-174) reported that *dulcius s. str.* most frequently raided ants including the leaf cutters, *Acromyrmex heyeri* and *A. silvestri*, and also raided *Polybia lechiquana*. On one occasion in Panamá *dulcius* was seen to avoid a struggling partly crushed calliphorid fly dropped next to a raid column. This isolated case may be significant since flies seem to be avoided or only rarely attacked by other species of *Eciton*.

A sample of almost 3,000 workers taken from an emigration column on 2 April 1956 was given three large larvae and two pupae of *Polistes* on the following evening. These were readily attacked, and immediately there was a noticeable amount of trophallaxis between adult workers. For this transfer of large drops of fluid, the mandibles of both workers were not used but spread apart while the other mouthparts held the drops. The workers seemed to clean each other more after the food was supplied, and this cleaning may have been initiated by workers cleaning food off the mandibles of other workers.

Compared with the activity of any of the other four common species of *Eciton*, the epigaeic activity of *dulcius crassinode* appears to be more confined to hours of dusk or darkness. The only diurnal record from Panamá is a raid column found at 5:00 p.m. However, Borgmeier watched a raid column of *dulcius s. str.* from 8:00 to 10:00 a.m. on 9 January 1934, but no locality or weather data was given (Borgmeier, 1955: 208). On Barro Colorado Island eight column raids of *d. crassinode* were found at night between 7:30 p.m. and 3:00 a.m. Since much more extensive searching for colonies was done during daylight, the scarcity of records for *dulcius crassinode* probably indicates that the species is even more nocturnal and subterranean than *vagans*. The interruption of an emigration at 5:40 a.m. and the presence of backtracking columns from about 5:00 p.m. to 6:00 a.m. are additional evidence that *dulcius* is active almost exclusively at night at least during the dry season and early rainy season. Although raids presumably always precede emigrations, there is no known way of predicting when the shift to an emigration may occur during a night. One colony, E-194, had raid columns continuously from 5:00 p.m. to after 10:45 p.m. when observations were ended.

On 24 February 1956 colony E-117 had a raid column which extended more than 100 meters and overlapped the area raided the previous day by *burchelli* colony E-111. The *dulcius* raid column probably followed the same trail as the emigration column of *burchelli* for short intermittent distances but clearly deviated from that trail in most places. The most striking result was that the raid column of *dulcius* entered a hole in the ground directly at the bivouac site used by the *burchelli* colony on the previous day. It would appear to be disadvantageous for one species of army ant to follow such trails of other species especially since the strongest and most easily followed trails would be in the areas most recently raided. The odor of the refuse deposit along with the arthropods found in it may have attracted the *dulcius* colony to the site, but it is not known how near the bivouac of the *dulcius* colony was to the site of the *burchelli* bivouac.

Emigrations of Eciton dulcius

Only five emigrations of *dulcius crassinode* have been observed. Four of these most likely started in the evening about 7:30 p.m., and the fifth, which was found at 3:30 a.m., probably started after midnight. Perhaps it is significant that the latter case was a colony with a brood of worker larvae approximately half grown, whereas the colonies which emigrated earlier had broods of callow workers and in one case a brood of eggs and young larvae. The total distance of an emigration has not been determined, but one colony emigrated at least 91 meters and another emigrated over 100 meters above ground. In all cases where columns were followed, they led to a hole in the ground, and the exact position or extent of each bivouac was not determined.

The emigration of colony E-204 which was discovered at 3:30 a.m. provides evidence of considerable importance for interpreting the movements of all colonies of subterranean army ants. Although it is not known when this colony started its emigration, on 4 July 1956 the emigration column was at its maximum development at 3:30 a.m. and extended from dense low vegetation at the edge of the laboratory clearing to a hole about 20 meters away in the center of the clearing. No attempt was made to trace the column back through the dense second growth to the old bivouac. After 5:00 a.m. the amount of brood being carried gradually decreased, while the per cent of smaller workers and the number of Phoridae increased, and by 5:40 a.m. the last ant had passed. After the last ant passed, four phorids ran along the emigration route. At 7:45 a.m. the same day there were no workers of <u>dulcius</u> at the hole into which the ants had disappeared earlier, and no columns were seen in that area of the clearing. The bivouac was partially dug out and a sample of almost 3,000 ants taken. About 5:00 p.m. a column gradually extended back along the previous emigration trail, and between 7:00 and 7:15 p.m. a strong column had developed continuing the previous emigration. Ants were carrying additional larvae to the same bivouac which had been partially dug out in the morning. This emigration column was only one to three ants wide or about half the width of the column in the morning. The number of ants emigrating fluctuated frequently during both observation periods, and at times the column stopped completely. In a few cases these fluctuations were partially due to my collecting, but at other times the interruptions started some distance before my collecting spot. At 7:41 p.m. the queen reached the observation point and was taken. She was accompanied by a small retinue of workers with only ten to 20 majors included in the retinue itself and among the guard workers one meter in front and behind the queen. At 7:45 p.m. the last brood passed the observation point, and at 7:51 p.m. the last worker passed. More Phoridae were again noticed near the end of the emigration column, and one passed after the last ant went by. Observations were continued for five minutes after the last ant passed, and then I followed the emigration trail in the direction of the old bivouac without finding any more ants or myrmecophiles. Between 8:00 and 9:00 p.m. there was a raid column extending in the direction approximately opposite to that from which the ants had emigrated to the present bivouac. No backtracking column had started by that time, but by 4:00 a.m. the following morning (5 July 1956) there was a column about one ant wide along both this new raid route and the backtracking route. At 8:00 p.m. the colony was found emigrating along a route almost parallel to that used in coming to the bivouac of 4 to 5 April. Backtracking columns were seen along the emigration and raid trails of colony E-204 in the laboratory clearing up until 10 July. These backtracking columns stopped daily about 6:00 a.m. and started again in the evening.

If the above divided emigration had been observed only in the evening, one might conclude that the entire emigration of an exceptionally small colony had been seen. Before colony E-204 was studied, colony E-143 had been found on 11 April 1956 at 7:30 p.m. while it had only a weak raid column. Between 7:30 and 8:00 p.m. there was a gradual shift to an emigration. At 8:30 p.m. the queen was taken as she was running along in a small retinue, and by 8:35 p.m. the last ants had passed the observation point. If this short emigration included an entire colony, it clearly was the smallest colony which I have ever seen for any species of army ant and must have comprised between 30,000 and 60,000 workers. However, the finding of the divided emigration of colony E-204 strongly suggests that during the preceding night colony E-143 may have started an emigration which was interrupted. Rain did not delay or interrupt this emigration for no rain fell during the entire preceding week. In addition, other facts indicate that the colony was following a strong chemical trail previously used either by a raid or emigration column. The raid column of colony E-143 advanced quite rapidly over the forest floor, and within a half hour the column changed into a strong emigration column. At the time the raid column was found the ants had not yet advanced across several meters which were used by the emigrating ants a half hour later.

The other two emigrations of *dulcius crassinode* which were observed (colonies '55 D-1.Mar. and E-137) were found about 8:15 p.m. after both columns were at their maximum emigration strength. The queens of these colonies were seen on the emigrations between 8:30 and 9:00 p.m. The emigration of colony E-137 lasted until 10:40 p.m. at the observation point; the other emigration was watched only until 9:25 p.m. Both these cases show timing similar to emigrations of *E. hamatum* but probably somewhat later in both their start and finish. The queen clearly emigrates near the end of the colony, and the colony size is probably close to that of *hamatum* on the basis of the meager evidence from the above emigrations.

Bivouacs and Refuse Deposits of Eciton dulcius

Although a number of columns of *dulcius crassinode* were traced to holes in the ground, pounding on the ground or shallow digging indicated that the bivouac probably was not near the surface. The only bivouac which was located was that of colony E-204 which was partially dug out at 7:45 a.m. on 4 July 1956 after the first part of the colony's emigration had been completed. The ants were in a depression which had been filled in by placing limbs of trees parallel to one another. No ants were on the surface when the digging began. Most of the ants were in clusters hanging from branches five to ten centimeters in diameter. Most of the nearly full-grown larvae were held up in the ant clusters, but many were widely scattered between the branches, under leaves, etc. There was no indication that the larvae were arranged according to size. The colony had columns going into holes which extended at least 30 cm. below the exposed part of the bivouac, but no digging was done deeper than 40 cm. No raid columns were seen throughout the day until a back-tracking column started about 5:00 p.m. and a small column extended about 50 cm. in the opposite direction. A few scattered pieces of booty refuse but no distinct refuse deposits were seen. Bruch (1923: 173) reported finding refuse deposits in three peripheral chambers of a leaf cutter ant nest which had been occupied by *dulcius s. str.* In this nest he found workers in upper chambers and larvae and cocoons in two lower chambers. Bruch (1923, 1934b) found that *dulcius s. str.* often bivouacked in abandoned or occupied nests of *Acromyrmex heyeri*, *A. silvestri*, *Atta* or *Cornitermes*.

Interrelations Among Individuals of Eciton dulcius

A total of four queens of *dulcius crassinode* have been taken, and all were removed from emigration columns. The dates and times when these queens were taken are given in table 1. These queens were all kept alive for observations in the laboratory, but like all *Eciton* queens they quickly died. Queen E-137 lived for six and one-half days in the laboratory with over 1,000 workers. This queen drank some water from cotton but never was seen to eat or to be fed by the workers although food was present in the laboratory nest. Queen E-204 lived for five and one-half days in the laboratory with less than 200 workers. All these workers, except for two majors, died before the queen. This result was in marked contrast to other *Eciton* queens from epigaeic colonies which died while most of the workers taken with them were still quite active. Circocyllibanid mites and limulodid beetles were present in the laboratory nests, but there is no clear evidence that the death of the workers was hastened by these myrmecophiles. Samples of workers of the more subterranean species usually outlived their queens taken at the same time, but the workers died more quickly than those of the epigaeic species, *burchelli* and *hamatum*. Workers from colonies of *dulcius* usually died sooner than those of *vagans* in laboratory nests; however, a sample from colony E-212 of E. *vagans* died at the same time as their queen after only three days in the laboratory. As in the other species of *Eciton*, large workers of *dulcius* usually lived longer than the small workers in the laboratory.

The queen of colony E-143 was placed in an empty nest 20 cm. square, and the nest was connected by a tube to a larger nest containing almost 3,000 *dulcius crassinode* workers from colony E-137 which had been in the laboratory without their queen for about 13 days. Sixteen workers immediately entered the nest with the queen and alternately climbed on her and ran around the nest. Only two attempted to sting the queen, and none bit or pulled her appendages. The workers readily licked her body and especially her gaster which may have had an excess of secretions or dirt on it since no workers had been with the queen for two days. The tube was clamped shut to prevent additional ants from entering the chamber with the queen. The positions of all workers which licked or kept their heads over a segment for at least two seconds are recorded in table 2.

These data are comparable to those recorded with *E. hamatum* and indicate that the workers are more attracted to the first two gaster segments and not to the anal region. None of the workers was attracted to the mouthparts of the queen. After 25 minutes about 60 additional workers were let into the nest, and when some of these started biting and stinging the queen, no further observations were attempted.

Eciton mexicanum Roger

Six subspecies of *Eciton mexicanum* Roger had been described on the basis of differences among the queens and males (Borgmeier, 1955: 250-261). The workers can be referred to a subspecies only on the basis of the locality where they were found or by association with reproductives. Borgmeier has described the subspecies *panamense* based on specimens from Barro Colorado Island and several other localities in Panamá. The male of this subspecies is not known. The subspecies *mexicanum* Roger is known from Costa Rica and México, and this is the subspecies discussed by Schneirla (1947) under the name *E. rogeri*.

Colony numbers were assigned to 31 colonies of *mexicanum* found on Barro Colorado Island from February to August 1956. However, this list probably includes about ten colonies to which two numbers were assigned, since no colony could be followed for its entire emigration. Nevertheless, *hamatum* was the only species of *Eciton* found more frequently (with 32 colonies recorded). Since *mexicanum* is the smallest species, has the narrowest raid columns, is most timid and is one of the more subterranean and nocturnal of the five common *Eciton* species, one would predict that fewer colonies would be found. The above data may indicate that *mexicanum* is either more abundant than *hamatum* or has more frequent or diffuse raid columns.

Raids of Eciton mexicanum

The most common booty seen being carried by Eciton mexicanum were larvae and pupae of ants and occasional adult ants. All raid columns except one were found on the ground or on objects close to the ground with little indication that this species raids up on any vegetation. The single exception, a raid column of colony E-135, extended at least six meters up a tree trunk, and numerous white larvae about 15 mm. long were being carried down the trunk between 8:10 and 8:40 p.m. On one occasion a colony was found attacking a large cricket more than two centimeters long. The cricket was being actively attacked by about 25 ants, but more than twice that number were standing quietly around the cricket. When a cicada, whose thorax had been crushed to prevent flight but not movement, was placed next to the same raid column, the ants did not attack it even when they touched the cicada. The same species of cicada was killed by L. coecus. Other large insects like beetles were not attacked, and the ants ran from them.

Compared with swarm raids or even column raids of hamatum, the raids of mexicanum are much less spectacular and often difficult to observe because they are hidden under leaves and other objects. Most of the actual attacking goes on underground in ant nests. The rate of progress for a large raid column was five meters in a half hour (between 8:45 and 9:15 p.m.). The same colony, E-151, also had two much shorter and less active columns branching from the base column. These branch columns and a number of other raid columns of other colonies advanced at a rate of about six to eight meters per hour. The distal ends of the raid columns of *hamatum* usually have small groups of workers which fan out slightly and sometimes look like miniature swarms of ten to 50 workers. However, the advancing columns of *mexicanum* show much less branching at their tips, often giving the distinct impression that the workers are following a narrow chemical trail. The fans at tips of columns sometimes were five to ten centimeters wide. Even after a chemical trail must have been well established by at least several hours use, the tendency to stay under fallen leaves was more pronounced than that shown by the other species of *Eciton*. When the leaf cover was removed, the column shifted a few centimeters to adjacent leaf cover. The smaller size of the workers of *mexicanum* would appear to be an advantage in raiding under objects. The majors are two to four millimeters shorter than those of the other four species of *Eciton*, and the other *mexicanum* workers are proportionately smaller. The shifts of columns occurred at night when the only light was from a flashlight. Air currents or some other factor may also cause such shifts. No measurements were made of light intensity, but *mexicanum* was more easily disturbed by light and attempts at collecting than any of the other species of *Eciton*. For example, a drop of saliva three millimeters in diameter caused a complete break in a steady raid column. The ants ran in opposite directions away from the drop but quickly resumed travel along the column with hesitation at the drop. Without any visible interference with a raid column, there were frequent fluctuations of traffic moving in both directions, and at times there would be gaps of a meter or more with no ants on the trail between spurts of activity.

Twenty-eight raid columns of *Eciton mexicanum* were found on Barro Colorado Island between the hours of 6:00 p.m. and 1:50 a.m. The only colony which was not found raiding at night was colony E-184 observed between 2:45 and 4:30 p.m. on 4 June 1956. Throughout the literature on various species of army ants there are many statements that these ants appear after rains. This case of a diurnal raid of mexicanum followed a a rainfall of 1.6 inches on 3 June and one of 0.26 inches on 4 June. On both days the rain was concentrated around midnight when it might have interfered with raiding. May was a moist month with 16.55 inches of rain, but the last rainfall of an inch or more before 3 June was on May 23. The lack of more afternoon records is perhaps due primarily to less field work at that time; however, extensive field work was done in the morning without revealing a single raid of mexicanum after dawn. The only exception to the total lack of epigaeic activity during the morning was a backtracking column of colony E-108 on 15 February 1956 in the early dry season. This column was found at 11:30 a.m. along the route of the emigration of the previous night. The column was a steady one, but the ants were scattered six to ten centimeters apart and were almost all under leaves. This column would not have been found if I had not known exactly where to look, since only an occasional ant could be seen without removing leaves. Likewise, considerable numbers of raid columns of mexicanum probably escaped notice because they were hidden under leaves.

Four raids were found between 6:00 and 7:00 p.m., and perhaps these were initiated near the time when the epigaeic species are beginning their afternoon resurgence following the siesta period. Since some nocturnal raid columns were weak but increased in strength while they were watched, it is probable that many raids are started after dusk.

In southern México mexicanum s. str. was found to have column raids "reduced to a minimum through the midday hours" (Schneirla, 1947: 5-6).

These ants were observed during the dry season, but they were fairly actively raiding throughout the day, and nocturnal raiding was not mentioned.

Although the epigaeic species, hamatum and burchelli, have been distinguished on the basis of their raiding and other behavior from the remaining species of Eciton, there has been no attempt to arrange the species within the subterranean group according to their behavior. Referring to all the subterranean species, Schneirla (1957a: 125) states: "These, although at times found in surface bivouacs under humid conditions in deep forest, at times carrying out full column raids on the surface, are persistently subterranean in nesting and often make extensive use of underground avenues in their raids and emigrations." Although workers carrying booty frequently can be followed back to holes in the ground, there is no good evidence as to how extensive the underground raid or emigration trails might be. On the basis of the large amount of nocturnal activity and the greater tendency for mexicanum to stay under leaves in its raiding, I would rank mexicanum as "more subterranean" than vagans and dulcius.

Colony E-197 had a raid column in the laboratory clearing which carried booty into the same hole between drainage tiles which had been used five weeks earlier by an emigration column of Neivamyrmex pilosus. Although these tiles and the foundation of the building limited the number of holes available, there were other holes and cracks in the vicinity. No other example is known in which mexicanum may have been following another army ant trail.

Emigrations of Eciton mexicanum

Six emigrations of Eciton mexicanum were watched on Barro Colorado Island for the following periods: 4 hours, 2 hours, 40, 15, ten and five minutes. The earliest emigration was that of colony E-170 found at 6:20 p.m. At that time less brood was being carried, and the column was slightly narrower than it was about 7:00 p.m. when the column reached its maximum width. Therefore, this emigration was probably seen within an hour of its start. The latest observations of emigrations were made on colony E-108 which still had a strong column at 11:35 p.m. about two hours after the queen had reached the observation point. This colony was found at 9:30 p.m. when the emigration column was at its maximum strength, and within ten minutes the queen was seen. Perhaps she emigrated relatively early rather than after 75 to 90% of the colony had left the old bivouac. Schneirla (1947: 5) found an emigration of mexicanum s. str. at 5:30 p.m. during the dry season in southern México.

Emigration columns like raid columns were normally found on the ground under leaves. However, on one occasion an emigration followed a slender liana which started at the ground and extended about 70 cm. above the ground at its maximum height. The ants followed this liana for more than two meters. The diameter of the liana was approximately five millimeters, and for most of its length the ants had made a flange ten to 15 mm. wide. Within the flange there were numerous mexicanum larvae, but it is not known whether they were feeding there.

Like the raid columns, the emigration columns of mexicanum were more easily interrupted than those of the other species of Eciton commonly found in Panamá. When we were trying to collect workers or myrmecophiles with forceps or aspirator, an emigration column frequently stopped completely with the ants running back toward the old bivouac. Light would also cause more disturbance of the column than was exhibited by emigrations of other species of *Eciton*. However, even when the light was kept constant and no collecting or other noticeable disturbance of the column was made at the observation point, the number of ants along the column varied more than was seen in other emigrations of *Eciton* except for one emigration of *dulcius*.

If one gently brushed the edge of the emigration column with forceps, major and intermediate workers including both guard and emigrating individuals would attack the forceps. Soon a group of six to ten workers would form a ball at the tip of the forceps, and this response could be facilitated by holding a worker at the tip. That worker evidently released some chemical which would arouse the other ants even without actual contact. Other species of *Eciton* reacted in a similar manner; however, only between three and five balls of *mexicanum* workers could be collected at one place along the emigration column; whereas many repeated collections of the more epigaeic species could be made. The workers of *mexicanum* would fan out on the ground like other species at the site of the disturbance, but then they would break the emigration column completely with workers running in opposite directions away from the disturbance.

No good estimates of the size of *mexicanum* colonies are available. Based on the partial emigrations observed, one would predict that the colonies are about the size of those of *hamatum*.

The only evidence available supporting the hypothesis of a nomadic-statary cycle is the type of brood seen in emigrations in Panamá and Schneirla's observations on the broods in bivouacs in México. (More details on the latter are given below under the section on bivouacs.) No eggs or cocoons have been taken from any emigration column. Colony '45 K studied by Schneirla (1947: 5-6) in México had a "single brood of well-advanced worker larvae" and emigrated on two successive nights. Four colonies, E-108, E-170, E-251 and E-256, all had broods of larvae with a total range in lengths of 1.2 to 7.6 mm. Callow workers were seen in the emigration columns of these four colonies and also those of colonies E-153 and E-239. As among other species of *Eciton*, callows of *mexicanum* were more likely to be carried in the emigrations than older workers. Judging from the callows seen in colonies which had some larvae between 6.0 and 7.6 mm., the smallest workers emerge last. At times when only slight differences in color could be distinguished among the majors, the smallest callow workers were a light yellow straw color contrasting conspicuously with the dark red-brown older adults. The range in color indicates that the workers of *mexicanum* emerge through a longer period than those of *hamatum* and possibly longer than those of *burchelli*. The three queens taken from emigration columns and the previous queens reported by Schneirla (1947: 5-6), Bruch (1934a: 125-127) and Borgmeier (1933: 96; 1955: 250) were all contracted when found. The lack of cocoons, presence of callows, presence of contracted queens and synchronous broods on emigrations all indicate that *mexicanum* has a nomadic-statary activity cycle comparable to *hamatum*.

On all emigrations there was a noticeable increase in excitement when the queen ran along the column, however, the retinues of workers were relatively small. On the emigration of colony E-170 there was no clear retinue even though the queen was not moving unusually slowly or quickly. Perhaps my disturbance of the column for about four hours before the queen passed had attracted most of the majors from the bivouac to my observation point. Most of the majors were not collected because it was impossible to do so without interrupting the emigration, and the majority had gradually moved toward the new bivouac. For at least an hour before the queen reached the observation point, between ten and 14 majors were constantly present as guards along the edges of the column. Although these majors did not have any direct contact with the queen as she passed, they reared their bodies upward and waved their front legs and antennae more quickly. The column did not widen and no ants rode on the queen. The other two queens were accompanied by more distinct retinues, but my collecting made it impossible to get an estimate of their normal size. The queen of colony E-251 was found running toward the old bivouac in the opposite direction of the retinue. This was probably due to effects of my light, since I had been collecting at this spot for only five minutes. The wave of excited workers making up the retinue passed on toward the new bivouac with no indication that the queen was not among the workers. The queen was collected before any of the majors or other workers could gather over her.

Bivouacs of Eciton mexicanum

Only a single bivouac of *Eciton mexicanum*, colony E-184, was located during this study in Panamá, and it was under the base of a tree where it was impossible to dig it out. The ants entered next to a buttress root, and a small cluster was within five centimeters of the surface of the ground. Pounding on the surrounding ground and pushing sticks down cracks caused several thousand ants to pour out of the bivouac. The raid columns had only dark workers on them; nevertheless, a large number of callow workers came out of the bivouac when it was disturbed. Unfortunately no brood was found although 1,522 workers were taken. Since callows were not participating in the raids to any extent, and since no larval brood was seen, this colony probably had just started a nomadic phase.

Scheirla (1947: 5-6) reported finding in México one statary bivouac of *mexicanum* *s. str.* inside a hollow log and another well-hidden bivouac in the remains of an old tree root hidden under vines and detritus. In Costa Rica a bivouac of the same subspecies was found by Nevermann under wood on the ground (Borgmeier, 1933: 96). In spite of much more extensive studies of army ants on Barro Colorado Island by Schneirla and others, no bivouac of *mexicanum panamense* has been found which was as exposed as those from Costa Rica and México. Perhaps these two subspecies have differing ecological preferences for bivouac sites, or the exposed bivouacs may have been found by chance in more moist places.

Other Species of Eciton

The remaining species of *Eciton* are either rare or absent in Panamá. Only brief comments or additional records are given for comparison with the other species. Omitted are two remaining species, *E. setigaster* Borgmeier and *E. uncinatum* Borgmeier, known only from a few males.

Eciton quadriglume (Haliday)

Borgmeier (1955: 199) has reported that *Eciton quadriglume* ranges from Misiones Province, Argentina northward to Perú and the state of Amazonas in Brasil. However, he also reports examining a specimen with the locality "Panama" (p. 198). Although the species of *Eciton* in Panamá rarely or never attack *Atta* and other leaf cutter ants, *quadriglume* apparently attacks these ants frequently (Reichensperger, 1924b). The bivouacs may be either epigaeic or subterranean. The males seem to be produced over a longer period of time than those of most species of *Eciton* and have been found during both rainy and dry seasons on dates from November to May (Borgmeier, 1955: 199-200; and my collection).

Eciton rapax F. Smith

Eciton rapax is a rare species known only from the workers found in central and northern Brasil, Bolivia, Perú and Colombia. Borgmeier (1955: 212) considers that *E. jansoni* is probably the male of *rapax*. *E. rapax* is of special interest because majors with hook-like mandibles have never been found even though large workers 13 mm. in length have been taken.

Eciton jansoni Forel

Eciton jansoni is known only from a few males taken in Nicaragua, Costa Rica, Panamá, Colombia and Equador (Borgmeier, 1955: 212). Borgmeier has considered this species to be the male of *rapax*. Because the distribution of *jansoni* extends much farther to the north overlapping that of *rapax* only in Colombia, it is more probable that *jansoni* is the male of *dulcius crassinode*. If this association can be proved, *crassinode* would become a synonym of *jansoni* which would remain a valid species. Males of *jansoni* have been taken from February to June, and thus, seem to be restricted to the dry season and early rainy season. Only two records are known from Barro Colorado Island: 31 May 1956 (C. W. and M. E. Rettenmeyer 1891) 1♂ taken at light, and May 1941 (J. Zetek 4800)

1♂. (I have not seen the latter specimen, but it is recorded under the name *E. velutatum* in the catalog of species found at the Canal Zone Biological Area.)

Eciton drepanophorum F. Smith

The only observations of the behavior of *Eciton drepanophorum* were made by Bates (F. Smith, 1858: 149; Bates, 1863, vol. 2: 356-357). Judging from these observations *drepanophorum* may be as epigaeic as *hamatum* since it attacks wasps and drives insects in advance of its raids. It may have swarm raids, because Bates reported ant birds accompanying its raids.

Labidus praedator (F. Smith)

Labidus praedator ranges from central México (state of San Luis Potosi) south to northern Argentina and is one of the most common species of army ants throughout its range. Borgmeier (1955: 111-113) has divided *praedator* into two subspecies (*praedator s. str.* and *sedulus*) which seem to be sympatric from Bolivia to Costa Rica. A few records indicate that the two subspecies are not ecologically separated according to elevation. Even though the species is common, the males have not been adequately collected to show the exact distribution of either subspecies. Workers were referred to these subspecies by Borgmeier (*l. c.*) on the basis of the shapes and sizes of the heads of major workers. However, these distinctions are difficult to see and of little value since there is no known way to determine which workers are the largest in a colony without collecting the entire colony. There does not seem to be any distinct morphological change between majors or soldiers and submajors such as occurs in *Eciton*. In addition, one can seldom collect the largest workers present in a colony since these never or only rarely take part in the raids. Borgmeier has referred all specimens from Barro Colorado Island to *praedator sedulus* Menozzi. The largest head width reported for workers (soldiers) of this subspecies is 2.8 mm. compared with 3.4 mm. for *p. praedator*. However, the largest workers we found on Barro Colorado Island have head widths under 3.0 mm., and the largest workers commonly seen have heads only 2.0 to 2.5 mm. wide.

The workers of *praedator sedulus* all have strong bites, and even the smallest workers could bite my skin more severely than workers of comparable size belonging to any other species of army ant found on Barro Colorado Island. However, the stings of the *praedator* workers in most cases could not penetrate my skin.

Raids of Labidus praedator

Labidus praedator eats different species of ants but never was seen attacking or carrying *Paraponera clavata*. Like *E. burchelli*, *praedator* appears to feed on a wide variety of arthropods, and Schneirla (1949b: 75) has reported that it feeds more on smaller organisms than does *burchelli*. Although a quantitative study has not been made, it is likely that *praedator* kills almost all the arthropods killed by *burchelli* on the forest floor, but less frequently kills the larger species such as scorpions. The minor workers of *praedator* are especially numerous and much smaller than the minors of *burchelli*. These tiny workers probably attack minute ants and possibly Collembola and mites. However, only a few mites (Oribatei) which appeared to have been bitten by ants have been found in samples of *praedator* taken from raids. Williams (1941: 116) reported that the minimal numbers of microarthropods which he recovered from forest floor litter were found in the two areas raided on the previous day by army ants, identified as *praedator* by Schneirla (1956b: 391).

If one judges from the recognizable booty in raid columns, ants are the most frequent prey. During 1956 we observed *praedator* also killing numerous other arthropods including: Isopoda, Amphipoda, Araneida and Orthoptera (Gryllidae, Tettigoniidae and Blattidae). It was seen to attack Scarabaeidae and Histeridae but abandoned these beetles after a few minutes with little damage to the beetles.

Like other army ants, *L. praedator* will attack vertebrates but seldom kills them. I have never seen this species feeding on any vertebrate, but Reh (1897: 615) reported finding a mouse covered with *praedator*. The mouse was still twitching and was bloody from the attacks of the ants, but it was not stated whether the ants actually stripped any flesh from the mouse.

Borgmeier (1955: 108) has given a brief review of unusual foods which *praedator* has been reported to eat or carry. Included are carcasses of dead animals, sugar, crushed pineapple fruit, boiled rice, palm fruit (*Attalea indaya*) and dried apple cuttings. It is not clear how many of these items the ants were actually eating and how many may only have been carried. In addition, the ants may have been attracted to these substances because of moisture on them; in fact, workers will readily lick and sometimes carry a small stick or other object which is moistened with water. *Labidus praedator* was found clustered more frequently than any other army ant on moist spots on the forest floor where leaf litter had been scraped away or where water was spilled.

This ant was also seen drinking droplets of dew on grass at night. In laboratory nests *praedator* would not eat peanuts, and I have found no reports of its eating vegetable oils of any kind. In marked contrast, *L. coecus* frequently eats these types of plant materials.

The raid swarms of *praedator*, like those of *burchelli*, are not as successful as one would conclude from the literature. Sometimes *praedator* entered the nest of a potential prey ant but would be successful in capturing only a few individuals. Most workers of the attacked species which ran out of their nest carried larvae or other brood and often escaped by running up vegetation where the *praedator* did not find them. *L. praedator* also did not cover the ground thoroughly, and numerous insects could stay quietly between anastomosing columns until the swarm raid had left the area. When a swarm raid of *praedator* did attack potential prey, it was amazing how quickly this small army ant could remove legs and tear up many arthropods. In a few seconds the army ants could remove all the legs from a cricket and have started pulling the rest of the body apart.

The basic pattern of a swarm raid of *L. praedator* is similar to that of *E. burchelli*; however, there are a number of significant differences. The raids of *praedator* are usually considerably smaller than those of *burchelli*, and the swarm front seldom exceeds four meters in width. A maximal swarm raid of *praedator* is about eight meters wide at the swarm front and has the same general shape as the swarm raid diagrammed for *burchelli* in figure 70. However, during the 1956 work in Panamá it was evident that maximal raids do not occur frequently, and when they do occur they may show the maximal development only a brief time. We never found a swarm raid of this species which lasted for several hours in the typical pattern of a burchelli swarm raid.

Wheeler (1921: 310-311) stated that raid columns of praedator are conspicuously broader and denser than those of other army ants. This would apply only to praedator raid columns of maximal size which are dense ribbons of ants about ten ants wide. Raid columns of this width occur also during maximal raids of burchelli. However, the raid columns of praedator which are most frequent are one to three ants wide.

Since the bivouacs are typically subterranean, it is usually impossible to find their exact location by following the workers carrying booty. When workers carry booty away from the swarm front, they may enter holes in the ground in five or more places only a few meters apart. As the raid progresses, new holes are used, and some of the older ones may be abandoned. The ants are constantly raiding on, or at least extending, underground trails at the same time as the ants advance on the surface. Many of the holes used are not more than one to three meters back from the swarm front, and thus the fan area of anastomosing columns is not as extensive as that of burchelli. A base column may be completely absent on the surface of the ground, but the steady flow of ants in and out of holes near the swarm front indicates that there is a continuous column to the bivouac. On several occasions base columns along the surface of the ground have been followed for more than 100 meters. Booty was seen being carried in one direction for the entire length of these long epigaeic columns. Ants carrying booty along the more common epigaeic raid columns which extended only one-half to three meters often carried booty in opposite directions on two columns. The shifting of columns used by the booty carriers and the conflicting directions of the traffic add to the difficulties of trying to locate the direction of the bivouac. As the swarm advances much booty is temporarily put in caches under leaves. The booty may be carried back toward the bivouac for at least two hours after the swarm raid has stopped. During this period hundreds of workers can often be found standing under leaves apparently doing nothing, and essentially no additional prey is attacked after the swarm raid stops.

When praedator raids subterranean ant nests, one would expect that much of the booty would be carried back to the bivouac along subterranean routes extended from the passages of the raided nest. Perhaps this is not the case since the majority of booty being carried along the epigaeic trails and seen in the booty caches is brood of other species of ants. At no time was brood of praedator found in any of the booty caches; however, there was only a single case where a raid column changed into an emigration column while it was being watched. Since most larvae of Eciton which are found in booty caches are dropped there only after the beginning of an emigration, one would not expect praedator larvae to be found in booty caches along raid columns.

Maximal raids of praedator may continue in approximately the same direction for more than 25 meters with a pattern similar to figure 70. However, it is more frequent to find the swarm raids of praedator shifting their direction. The smaller swarm raids usually were the ones which showed the greatest tendency to change direction. In a similar manner small swarm raids of burchelli were diverted more sharply to one side or the other. Typical diagrams of two partial swarm raids of praedator are shown in figures 71 and 72.

The swarm raid of colony E-230 shown in figure 71 was found at 9:55 a.m., and the ants were advancing rapidly without finding a noticeable amount of booty. During the one and one-quarter hours that this swarm raid was observed the ants made four major shifts in direction. The fine dotted line indicates the maximum extent of the ground covered by the ants. Each arrow shows the position of the swarm at the time indicated with the swarm front near the head of each arrow. In addition to the major shifts, there was constant irregular back and forth shifting within the width of the swarm front. Three small trees may have influenced the direction of the swarm raid to some extent, but other trees within the area raided had no visible effect on the path of the ants. (These other trees are not shown in the diagram.) The abundance of booty may be one of the most important factors influencing the direction of these raids. Since a high percentage of the booty was hidden in caches under leaves, it was difficult to determine the source of most of the booty.

In two areas shown in figure 71 the progress of the ants was slowed. The stippled depression shown in the center of the diagram was entered by ants about 10:40 a.m.; and even though many ants continued beyond it at 10:50 a.m., other ants raided there extensively during the next half hour. The moist leaves in this depression may have attracted the ants as much or more than booty found there. The brush heap outlined by the broken line at the left of the figure also slowed the progress of the ants while thousands of workers dispersed upwards into the tangle of branches, vines, etc. At 11:10 a.m. the advance of the ants could no longer be followed because of the difficulties of working in this tangle of vegetation. There were at least five temporary columns along which booty was seen carried, but only the last one observed is indicated in the figure. Colony E-230 may have shifted its raiding toward the west due to the downward slope of the ground in that direction. The David

Fairchild Trail follows a contour line at that spot, and the ants moved parallel to it at first. About 10:15 a.m. they moved directly down the slope; but around 10:25 a.m. the swarm had a distinct fork, and part of the ants moved up the hill to cross Fairchild Trail again, and part of the ants turned down the hill. Raids of other colonies show similar patterns indicating that the slope of the ground is of much less importance than the amount or type of booty or the vegetation cover for influencing the direction of the raids of praedator.

The swarm raid of colony E-220 diagrammed in figure 72 was found at 10:00 a.m. on 25 July 1956 while the raid was moving southward across a fairly level area. In a few minutes a noticeable shift in traffic started toward the west, and it soon became clear that this was the main direction that the swarm was heading. For no discernible reason the ants decreased on the southward movement gradually stopping all advance in that direction shortly after 10:30 a.m. In a few places it appeared that trees may have influenced the direction of the ants, and these trees are indicated on the figure. After almost an hour in which the ants raided primarily toward the west, they shifted more toward the north. By 11:00 a.m. it was clear that the raid was slowly decreasing in strength. The workers decreased in number and seemed to be moving more slowly. Shortly after 11:00 a.m. it became difficult to distinguish a swarm front or any area where the ants were actively advancing. After 11:15 a.m. almost all the ants were tearing up booty previously caught, carrying booty back along trails, running along trails without booty, or just standing quietly.

The primary trails used by ants which were carrying booty are indicated by the broken arrows in figure 72. The first one labelled A was used extensively between 10:00 and 10:30 a.m. with subsequent traffic decreasing until about noon. Since this trail went almost due south, one might think the bivouac was in that direction. However, about 11:30 a.m. the next column used had ants carrying booty toward the northwest, and traffic on the subsequent columns went south and southeast. Around noon all four columns had ants on them carrying booty into the respective holes. When the ants retreat into a hole in the ground, the end of the raid column is quite similar to the end of an emigration column of Eciton. The last ants on the column run back along the trail in a manner almost as hesitant as that of the ants which are advancing the swarm front.

In the upper left part of figure 72 it can be seen that the ants completely reversed their direction of progress and doubled back over much of the same area previously raided. This reversal of movement or circling back over the same area results from a continuation of the more zigzag manner of raiding by praedator. Parts of a swarm raid of burchelli may circle back over the same area raided only a few minutes before, but such a route is much more distinct with praedator since the entire swarm raid or most of it is included.

Labidus praedator probably raids extensively underground judging from the number of columns which enter and come out of holes even where there are no ant nests which are being raided. This army ant also raids under leaves more than the five species of Eciton observed, with the possible exception of E. mexicanum. The smallest workers, about two millimeters long, can be seen running into holes and cracks which are much too small for the largest workers. Like other army ants, praedator digs readily and will enlarge holes until the larger workers can go through them.

In addition to its subterranean raiding, *praedator* also raids up trees and buildings. However, this army ant usually went only about two meters above the ground and never was seen to go higher than three meters. When *praedator* raids in low shrubs and trees, it does not cover the vegetation as thoroughly as does *burchelli*.

Seventeen *swarm* raids of *praedator* were found at various times throughout the day between 9:00 a.m. and 10:10 p.m. Although swarm raids probably occur at all times of the day, the data are inadequate to determine whether there is a tendency to have raids during any particular period. Raid columns were found at all hours of the day and night. The more frequent appearance of *praedator* either during the rainy season or after rains has been known for many years (Sumichrast, 1868: 40; Ihering, 1894: 381-383) and was supported by Schneirla's observations in México and Panamá (Schneirla, 1947: 10-11). Based on the amount of time we spent searching for army ants during 1956, swarm raids of *praedator* were at least twice as abundant during the rainy season as in the dry season.

In view of the fact that *praedator* is found more frequently during the rainy season, one might expect that the ants would have a siesta period or would never raid between noon and 3:00 p.m. However, we found two maximal swarm raids between noon and 3:00 p.m. in the middle of the dry season during February and March. Moreover, other raid swarms stopped advancing at different times during the day without any obvious connection with environmental factors, except in the case of heavy rains which would halt all raiding activity. Probably a colony has a number of small epigaeic raid swarms during each 24 hour day.

These may be widely separated without any epigaeic connecting columns. Adjacent raid columns of *praedator* were found on only one occasion in 1956, and these were considered to belong to two colonies (E-182, E-183) since no connection between them could be found.

Many arthropods were driven in front of the swarm raids of *praedator*, and flies were invariably abundant over diurnal swarm raids but absent over the nocturnal ones. These flies are the same species or closely related to the species of Tachinidae and Conopidae which accompany the swarm raids of *burchelli*. The ant birds were present near some of the larger diurnal swarm raids, but they were more frequently absent, probably because of the small size and short life of most *praedator* swarm raids.

Emigrations of Labidus praedator

Emigrations of *Labidus praedator* have been seen infrequently, and no queens have been taken from emigration columns. During 1956 we found two columns which appeared to be emigrations, but in both cases only a small part of the colonies must have been seen. The first case was colony E-177, first seen at 7:10 p.m. on 29 May 1956 when it had a raid column carrying booty into a crack in a concrete drain. This column may have been the start of an emigration since at 6:45 a.m. the next morning there was a much stronger emigration column along the same trail. The column in the morning was considered to be an emigration column since there were myrmecophiles running in it, numerous guard workers were present along the margins, and the traffic was strong and consistently moving in one direction. The column was continuously three to five ants wide, well below the maximum strength of about eight ants wide for emigrations of praedator, and no brood was seen being carried. At 7:57 a.m. there was a complete break in the traffic at some underground point toward the old bivouac. When the traffic stopped, all the guard workers immediately left their positions and moved toward the new bivouac. The column resumed after an interruption of five minutes and quickly regained its former strength. Within the next half hour a few guard workers lined up along the route but not as many as had been present earlier. The column continued at the same strength until rain interrupted it between 9:40 and 9:45 a.m., including three minutes of heavy rain when no ants were seen. When the shower stopped, the column again continued; however, about 10:00 a.m. the traffic decreased to half its previous strength. During this period the sun was becoming stronger, and by 10:30 a.m. the column was partially in bright sunlight. The ants continued to emigrate at an estimated rate of 300 to 500 per minute which was somewhat less than half their previous maximum. Between 10:50 and 11:00 a.m. the sunlight reached its maximum brightness, and the ants stopped emigrating completely. Several myrmecophilous millipeds and possibly 100 workers were seen to enter the area where the sun was shining brightly on the trail, and then they turned and ran back toward the old bivouac. The ants did not continue this emigration in the evening of the same day. However, they may have emigrated later that night because they were never seen again.

This emigration column of colony E-177 extended only about four meters on the surface of the ground. The total emigration distance probably was much greater, but neither the locations of the bivouacs nor other columns of praedator could be found in the vicinity. The first meter of the column closest to the old bivouac went through grass, and walls of loose dirt had been constructed for stretches of ten to 20 cm. along both sides of the column. The workers piled moist dirt particles up to make these walls and probably did not add any substance to the dirt to hold the particles together. There were a few places, including one almost 20 cm. in length, where a complete tunnel of dirt had been constructed. Figure 8 shows the walls of dirt and a short stretch where there is a complete roof connecting the walls. Guard workers were standing along the inner surfaces of these walls with their heads facing out along the open top edges. In some short sections the workers formed a partial or an entire tunnel with their bodies. Occasionally a worker could be seen to add a piece of dirt to the walls, and when a short stretch of the wall was broken down, part of it was immediately replaced. This species of army ant has also been seen to make tunnels and walls of wood fragments (Calvert and Calvert, 1917: 307-308).

It is not clear why the walls or tunnels were constructed in some places and not in others. In the three cases known to me the walls were made along the section of trail where the ants left a subterranean route and started an epigaeic one. Although the type of soil looked identical along the trail immediately following the dirt tunnel made by colony E-177, there was neither a tunnel made up of workers nor an increase in the number of guard workers at any time. In contrast to our observations, Calvert and Calvert (_l. c._) reported there were many more guard workers which formed walls and a tunnel with their bodies along the column where the dirt tunnel was absent.

An emigration of part of colony E-183 was observed, but the traffic several times moved in the direction of the old bivouac or was equally divided toward the old and new bivouacs. The colony either failed to emigrate or it emigrated by a different subterranean route rather than by the first epigaeic route. The shifting traffic was similar to that seen along columns of Eciton when colonies are dividing. At the same time that the emigration column was observed there were several raid columns near by which were not connected with the emigration column, and booty on these was being carried to holes more than 25 meters away from the emigration column. Perhaps all these columns belonged to the same colony, but the raid columns were considered a separate colony (E-182). At 6:45 a.m. on 3 June colony E-183 continued its raid along the same trail from a bivouac probably located at the edge of the laboratory clearing near the dock. This colony raided throughout the day around the laboratory buildings with increasing numbers of ants moving up the hill and going under the foundation of the old laboratory where small clusters could be seen at the northwest corner during the evening. The ants actively raided through the most open parts of the clearing during the entire day which was cloudy. Between 11:00 p.m. and midnight 1.51 inches of rain fell, and most traffic along the column must have been interrupted. By 1:00 a.m. on 4 June the rain had ended, and at 2:45 a.m. a strong column was moving up the hill toward the old laboratory. However, all booty except an occasional piece was still being carried down the hill. Between 7:00 and 7:55 a.m. on 4 June there was a noticeable increase in traffic up the hill, and more than 50% of the booty was being carried in that direction. At this time the colony was considered to be starting an emigration. Similar traffic with occasional spurts in either direction continued on the column until 10:40 a.m. when the column had greatly decreased in strength and observations were interrupted. The morning was predominantly cloudy, but several brief periods of sunlight seemed to cause a reversal in the "emigration" traffic. Myrmecophiles were seen in this column and were most abundant between 7:55 and 8:55 a.m. At 8:45 a.m. a dealate male was found in the column with so many workers clinging to it that it could scarcely walk. It is not known whether the male was emigrating with the colony or whether it had gotten into the column during the night. During the evening of 4 June the activity on this same column again increased and continued throughout the night with the prevailing traffic frequently changing back abd forth. On 5 June there was similar traffic on the column, and five larvae 3.2 to 4.0 mm. long were taken. The colony apparently emigrated in a different direction sometime during the night of 5 June since on the following day no praedator could be found around the old laboratory or along any of the trails where they had been seen previously. These observations indicate that colony E-183 either did not emigrate or emigrated only a short distance for two nights at a time when there was a larval brood.

Bivouacs of Labidus praedator

Bivouacs of Labidus praedator are as rarely found as emigrations. Nests have been reported to be found at great depths with openings 50 or more paces apart on the surface (Rengger, 1835, as reported by Ihering, 1894: 330), but no excavations have been made to substantiate how close any part of the bivouac is to these holes. Three bivouacs were probably located under the foundations of the laboratory buildings on Barro Colorado Island. A third bivouac (colony '52 P-7) was found in a rotten log about 55 cm. in diameter and extending at least 15 cm. into the soil beneath the log. A bivouac of E. hamatum (colony '52 H-A) was within a cavity of the same log. The *hamatum* were about 60 cm. from the *praedator*, but when I completely cut apart the log to attempt to collect the brood and queen of the *praedator*, there was little fighting between the two species. No queen was found, but 154 males including a single dealate were seen in the bivouac. (Borgmeier [1955: 83, 110, 113] states that three males were found in this nest. The total found was 154, but only three were sent to Father Borgmeier.) A total of 147 males was taken alive, and many of these subsequently lost their wings in the laboratory even though they were not allowed to fly. The immature brood consisted of eggs, young larvae and cocoons. Eggs were concentrated in three long chambers which were so narrow that it is unlikely that the queen could have laid them there. Cocoons were in the opposite side of the log primarily in one larger chamber, and larvae were scattered throughout the log in many chambers. The adult males were primarily in cavities in the ground, but a few were in the largest holes in the rotten log. When the males were dug out, it was clear that the largest workers were near the males, and these workers became unusually excited as the workers and males were collected. A large part of the bivouac must have been deeper in the ground, and probably the queen was in this section. At the time the bivouac was examined there was no raid column of *praedator* within ten meters of the log.

Bivouacs of *praedator* have also been found in a log and in a nest of *Solenopsis geminata* (Schneirla, 1947: 9), under a log and in two nests of *Cornitermes* (Luederwaldt, 1918: 57), under a small bridge made of logs and dirt (Sumichrast, 1868: 40), under foundations of buildings and in abandoned termite nests (Ihering, 1894: 330; Borgmeier, 1955: 108-109).

Colonies of praedator probably include over one million workers and possibly are the largest colonies among species of Ecitonini. Compared with species of Eciton, there is a much greater tendency for one to underestimate the number of praedator workers due to their small size. For example, a circular column of "several hundred" workers actually included almost 2,000 ants as can be determined from counting the workers in the drawing made from a photograph of the column (Schneirla, 1944a: 7). Based on one sample of 7,550 workers (colony E-146) aspirated from clusters at the edge of a bivouac under the foundation of the old laboratory there are about 15,000 workers per 100 ml. (compared with 3,000 to 6,000 workers of E. hamatum). Observations of emigrations and bivouacs indicate that the broods are also immense (Schneirla, 1947: 9), but no estimates have been made.

Sexual Broods of Labidus praedator

Only two cases have been reported in which a sexual brood has been found in a colony (Borgmeier, 1955: 109-110). Rev. P. Schwarzmaier found 12 winged males in a bivouac at Campinas, Goiás, Brasil, on 12 September 1935. The second case is the one mentioned above in which one dealate male and 153 winged males were found on 19 March 1952 in a bivouac of colony '52 P-7. In addition, there are two cases in which a single dealate male has been found in a column of workers: on 21 October 1905 Fiebrig found one at San Bernardino, Paraguay; and on 4 June 1956 one male was found in colony E-183 on Barro Colorado Island. Males of praedator frequently have the genitalia extruded and widely spread when they are found at lights. Since the genitalia of most of the males taken in the bivouac of colony '52 P-7 showed this same condition, the extrusion of the genitalia is probably not dependent upon flight, though it may occur only after a maturation period. No other species of Ecitonini showed such a pronounced extrusion of the genitalia.

In addition to the above records, males were taken at lights on Barro Colorado Island on the following dates (with the number of males in parentheses): 30 March 1955 (2); 31 March 1955 (3); 20 February 1956, 5:00 a.m. (2); 4 April 1956 (1); 26 April 1956 (1); 3 May 1956, 4:30 to 5:00 a.m. (1); 29 May 1956 (1); and 6 June 1956, 5:15 a.m. (1).

Although lights were run nightly until 19 August 1956, no additional males were taken. The above dates extend from 20 February to 6 June 1956 indicating a flight period of about four months starting during the dry season, with an apparent increase in numbers at the beginning of the rainy season. For comparison, the flights of males of *hamatum* and *burchelli* extended about two months (9 May to 4 July and 17 March to 11 May). Borgmeier also stated that the time of male flights of *praedator* is quite irregular, and the additional dates cited by him for Panamá and Costa Rica fall within the period indicated above.

Activity Cycle of Labidus praedator

There is conflicting evidence regarding the amount of nomadism shown by *Labidus praedator*. Several authors have stated that *praedator* has permanent nests ("Dauernester") or at least stays in the same nest site for from several months to three years (Ihering, 1894: 382; Sumichrast, 1868: 40; Luederwaldt, 1918: 57-58; and Borgmeier, 1955: 108-109). Several of these cases may be instances where a colony has left a site and subsequently the same species again bivouacked there. On three widely separated dates we have seen bivouacs, or large clusters of *praedator* which could be confused with bivouacs, at the northwest corner of the old laboratory building on Barro Colorado Island. No bivouac sites were ever seen under or close to any of the other buildings in the clearings. It is possible that this one corner was used frequently because water was spilled every day in this area next to the kitchen. The army ants used at least four routes in going to and from this one site. However, Sumichrast (*l.* *c.*) reported watching *praedator* every day for three months as the army ants were digging under a small bridge made of logs and dirt. In this case the ants were no longer at the site on 30 September, but about four months later a colony reappeared for a short duration. These observations were made in México during the summer months when one might expect the ants to be most nomadic. All our observations in Panamá support the hypothesis that the ants migrate frequently but perhaps more irregularly than species of *Eciton*.

The evidence on the degree of synchronization of the broods is similarly conflicting. The most clear evidence for synchronous broods paralleling those of *hamatum* has been presented by Schneirla (1947: 9) for colony X1 which had one large brood of "newly transformed" worker pupae [= young pupae or young callows?] and a second brood of eggs. However, a second colony reported by Schneirla (*l.* *c.*) appeared to have only a single brood of pigmented pupae close to emergence. Moreover, Schneirla (1957a: 125) has reported that four emigrations of *praedator* have been observed "in which ran tens of thousands of callow workers, with great numbers of unopened small cocoons being carried along." If these last five cases were to correspond to the typical *hamatum* pattern, a second brood of eggs or young larvae should have been present in each colony. It is possible that it could have been overlooked in each case or the young brood may have been in a different part of the emigration.

In contrast to the above cases of apparently synchronous broods, there are two examples of apparently nonsynchronous broods. Colony '52 P-7 had one brood of alate males, plus thousands of eggs, larvae and worker cocoons. The males must have been produced in this colony since they were winged and there were so many of them. One would expect to find only worker larvae along with such a brood. My samples of the brood was not as extensive as would be desirable to indicate the true proportions of the different ages. However, it includes about 300 eggs, 193 larvae ranging from 4.4 to 6.8 mm. in length, nine cocoons containing worker prepupae ranging from 3.2 to 8.0 mm., and two cocoons containing young pupae 3.2 and 8.8 mm. in length. Thus, mature pupae and callow adults were the only stages missing. The above measurements also indicate that the largest worker larvae did not spin cocoons first as there is a complete overlap in size among enclosed and unenclosed brood.

The latter case is not unique in that Luederwaldt (1918: 57-58) described a bivouac in which there were eggs, larvae 3.0 to 7.0 mm. in length, and light brown pupae 2.5 to 8.5 mm. in length. He also found innumerable empty cocoons 20 mm. long and 7 mm. wide which he thought were those of males, but no males were still in the bivouac, A similar case of nonsynchronous brood will be discussed under _L. coecus_ below.

Labidus coecus (Latreille)

According to the interpretation of Borgmeier (1953; 1955: 86) about 20 specific and subspecific names are synonyms of _Labidus coecus_, and he has recognized no subspecies even though he was convinced that subspecific names could be used on the basis of differences shown among three queens. The large number of names used for coecus is in part attributable to its range from the southern United States to Argentina. It is clear from examining males from widely separated localities such as Texas, Panamá and Argentina that the color and morphological variation found among specimens of coecus is considerable and probably at least as great as that shown by other subspecies of Ecitonini considered valid by Borgmeier. In spite of the fact that males of coecus are the most common males of Ecitonini found at lights, the males have been found with workers on only two occasions (Borgmeier, 1955: 92). Queens taken with workers have been reported from four localities: México, Costa Rica, British Guiana and Argentina.

Colonies of Labidus coecus, like those of praedator, appear to have semipermanent nests, judging from one colony which occupied an abandoned termite nest and the soil below it for more than four months (Ihering, 1912: 228). Wheeler observed coecus on numerous occasions in Texas but could not find a bivouac. Brues (1901: 353) reported finding one bivouac in Texas which "extended under stones for a distance of nearly twenty feet...."

No bivouac of coecus has been found on Barro Colorado Island, and the bivouac found by Neal A. Weber within a large rotted tree stump in British Guiana is the only one which has been described in any detail (Weber, 1941). It is noteworthy that the queen in this colony was physogastric and laid eggs for two days after which her gaster returned to the contracted condition. Weber reported that in addition to eggs he found "very young larvae" and pupae. I have examined about 500 specimens of brood taken by Weber from that colony and have found larvae ranging in age from those at hatching to mature larvae including some within cocoons. In addition, there were pupae which appeared to be of all ages and even some recently emerged callows.

A total of five physogastric and two contracted queens of *coecus* are known according to the summary by Borgmeier (1955: 82-83). These data together with that from the bivouac found by Weber suggest that the queens of *coecus* remain physogastric for a longer period than those of *Eciton* spp. They must lay eggs over a period of at least three weeks in order to produce a nonsynchronous brood such as found by Weber, but it is unlikely that the queens lay eggs continuously. The two contracted queens probably were found between their oviposition periods, but they may have been virgins. Unfortunately, since the dates when these two queens were taken are not known, it is impossible to tell whether these queens were taken at the time of year when sexual broods are produced.

No detailed descriptions of emigrations have been published; however, a few long covered columns mentioned in the literature may have been emigration columns. Brues (1901: 353) stated that *coecus* "moves only by tunneling underground," which is probably true for the most part. However, epigaeic nocturnal emigrations probably take place on rare occasions especially under humid tropical conditions and with the use of tunnels made by the ants.

Labidus coecus perhaps feeds on a greater variety of substances than any other species of Ecitonini. Like other army ants it primarily eats arthropods. However, *coecus* does not seem to prey as extensively on ants as do the other army ants which I have seen. On Barro Colorado Island *coecus* was observed feeding on Amphipoda, Araneida, Scarabaeidae, Cicadidae, Mantidae, Tettigoniidae, numerous moths belonging to a number of families, and several species of small ants. Most of the larger insects were attacked below a wall which had a strong light for attracting male Ecitonini and other insects. The army ants attacked about five to ten times the number of insects which they actually killed at the light. Even when an insect was killed, the ants sometimes abandoned it without doing any visible damage or after removing only part of the appendages. Vibrating these dead insects with a pair of forceps would usually result in a renewed attack on the part of the *coecus*.

In addition to the above insect prey, *coecus* has been reported to eat insect larvae and adults found in and under logs, cow manure and carcasses of dogs, cats, cattle or other animals (Wheeler, 1910: 264; Lindquist, 1942: 851-852). It is problematical whether or not the ants eat any part of the carcasses themselves. Wheeler (1908: 409) reported that *coecus* feeds on carrion, but later (1910: 264) he stated only that the ants were ferreting out larvae in dead bodies. It has been shown conclusively that *coecus* is an important predator on larvae of the screw-worm, *Callitroga hominivorax* (Coquerel) [= *Cochliomyia americana* (Cushing and Patton)], and other Diptera larvae living in the carcasses. In Texas *coecus* was considered to be the most important species of ant responsible for reducing the number of adult flies emerging from carcasses from about 93% to 4%. Not only did the ants kill larvae on carcasses, but *coecus* even attacked larvae in wounds of animals which were "down but not dead." The army ants also killed "scattered larvae dropped to simulate larvae escaping from wounds while the animals were still alive but per cent of adults from these rose to about 20%." On one occasion *coecus* was seen catching adult blowflies on the carcasses (Lindquist, 1942: 850-852).

Labidus coecus apparently eats more plant material such as seeds and cooked rice (Borgmeier, 1955: 93) and nutmeats of various kinds than does any other species of Neotropical army ant. Wheeler (1910: 264) reported that he "attracted and trapped great numbers of workers by burying a few walnut or pecan kernels in the lawns near Austin." Colony E-165 was found on Barro Colorado Island as the ants were carrying off peanuts dropped by some monkeys in their cage. The workers appeared to be able to smell a salted peanut placed one to three centimeters away from their column and ran up to it. When worker ants came in contact with a nutmeat, they vibrated their antennae more quickly, bit at the nutmeat and tried to pull it toward their bivouac. One half of a peanut kernel was too large for six of the small workers to move it more than a slight amount. Some of these workers ran back along the column, and soon workers with larger heads came and tugged at the peanut. When these were similarly unsuccessful, the biggest workers with huge heads appeared; and these, along with numerous workers of all the smaller sizes, dragged the peanut toward the bivouac. The maximum number of workers seen to pull a half of a peanut kernel was 12. Some feeding was done on the peanut in the course of pulling it around. However, most of the feeding was done underneath a covering of loose dirt piled over, but not actually touching the peanut. Although workers from this colony, E-165, readily attacked the peanuts, ants from three other colonies of *coecus* showed little interest in peanuts placed next to their raid columns.

The entire length of the epigaeic raid column along which these ants carried the nutmeats was about 2.2 meters. The ants came out of a hole in the ground, and the first 20 cm. of trail extending from the hole was covered by a tunnel of dirt like that described above under praedator. (Both species of Labidus had these tunnels primarily along their trails closest to the holes where the ants disappeared into the ground.) Between 1:30 and 7:30 a.m. this tunnel was extended 50 cm., and it was enlarged in several places. The construction of this tunnel was so rapid that the ants would have been able to completely enclose the entire length of their raid column during the period when it was observed. However, tunnel building was sporadic, and in some cases it was impossible to determine what might have initiated this activity. Twice I saw workers drag a half of a peanut kernel to the tunnel which was too small for both the peanut and the ants pulling it. The ants dropped the peanut and enlarged the tunnel before making a second attempt. After several attempts to get one piece down the tunnel, the ants dropped it and built the tunnel out around the nutmeat.

When coecus finds large insect prey which is not readily carried by one or a few ants, it also builds a dirt covering over it. The largest of these dirt domes were about one centimeter in height and five centimeters across with no supporting pillars. These dirt coverings are undoubtedly an important adaptation protecting the ants from desiccation. Around 7:00 a.m. when the sun started shining on the area of their raid, the workers no longer were seen in the open, but they continued their activity under the dirt coverings. By 8:00 a.m. the ants had withdrawn even from these tunnels and were active only under a brick and in a well-shaded section of the tunnel. The army ants also constructed a wall of dirt around the edges of the brick and repaired this wall after the brick had been lifted. No raiding activity was seen along part of the edge of the brick, but nevertheless, the wall was replaced. Perhaps this species of army ant is highly sensitive to air currents. When the ants withdrew from the more exposed parts of their raid columns, they abandoned a large proportion of the food. It is true that I supplied them with about 15 halves of peanuts and 12 large insects which is probably more than they would find in most places; however, it suggests that *coecus* may frequently abandon a large amount of food which they kill. On two occasions *Pheidole* sp. finished eating the food as soon as the army ants left it.

Five cicadas ranging in size from three to five centimeters, two May beetles about two centimeters long, and two tettigoniids were placed among the ants. These were all promptly killed primarily by biting. *L. coecus* rarely appears to sting its prey and also does not pull the appendages out straight or pull them directly off the prey as do species of *Eciton*. Compared with *E. burchelli*, *coecus* was much quicker at dissecting the large cicadas and scarabaeids. Even the smallest worker can give a person a bite which is easily felt except where skin is quite thick. A single insect about five centimeters long would have at least 200 workers attacking it and covering every surface except some broad smooth hard surfaces such as the elytra of beetles. When a large insect being attacked by numerous ants was quickly picked up, from 50 to at least 100 workers remained in the exact spot where the prey had been. These workers, like guard workers, reared up with their bodies vertical and constantly waved their front and sometimes their middle legs while rapidly vibrating their antennae. The workers remained in this position for at least five minutes. A large amount of raiding activity near by did not cause a decrease of excitement among the workers around the previous location of the prey but lengthened the time they would stay in their erect position to at least 15 minutes.

Since *coecus* is also attracted to vegetable oils, perhaps the attraction to nutmeats can be attributed to the oil in them. In Costa Rica, furthermore, a large number of workers became trapped in lard which they apparently tried to eat (C. W. Palmer, in letter). Although *coecus* will readily bite people and presumably attacks all vertebrates in the path of its raids, I know of no good evidence that this species actually eats any vertebrate. Weber (1941: 326) reported that *coecus* killed 22 young chickens in British Guiana, but he gave no indication that any parts of the chickens were eaten.

Raids of *Labidus coecus* are somewhat intermediate between swarm raids and column raids. Epigaeic columns are rare, and when present for either a long distance or for more than a few hours, the columns are probably covered by dirt. Bates (1863, v. 2: 365) claims to have followed their tunnels occasionally for a distance of one or two hundred yards. It is most probable that such long tunnels were used for emigrations. In Panamá, the typical raid consisted of ants pouring out of from one to over 20 holes in the ground. These ants would form a small swarm on the forest floor and were never seen to go higher than five centimeters on vegetation or on a building. The swarms observed showed little progress in any direction over a period of several hours, possibly because of abundant food in close proximity to the holes. Raid columns were observed between sections of the raid swarm and adjacent to the swarm, but no columns longer than eight meters were seen. The raid swarms often consisted of a number of rather dense masses of workers only ten centimeters wide advancing across the ground and connected by a column less than a meter in length extending to a hole in the ground. A large number of these small masses or swarms connected to branching columns extending to numerous holes would comprise the entire swarm raid. The lack of a distinct direction of progress made these raids of *coecus* appear much more disorganized than those of *praedator*. The *coecus* raid swarms expanded on the surface of the ground, and then all the workers gradually retreated into the ground possibly to again emerge on the surface at some distance away. It would seem unlikely that these retreats indicated the end of a raid when they occurred in the middle of the night. Since *coecus* was rarely seen on Barro Colorado Island, each raiding site was rechecked at least on the following night, and several of the areas were searched several times the same day and following days. In all cases after the ants had disappeared, they did not reappear even though peanuts were put at the sites for bait.

Raids of *Labidus coecus* were rarely seen on Barro Colorado Island probably because of the following four characteristics: the raids are (1) seldom on the surface of the ground, (2) primarily nocturnal, (3) small in area, and (4) short in duration. Seven raids of *coecus* were found between 18 May and 29 July 1956, whereas none were found between 11 February and 17 May. Since more time was spent searching for colonies during the latter period, these data indicate that *coecus* is more commonly seen during the rainy season.

The earliest observation of a swarm raid of coecus was at 7:45 p.m. The latest records of activity in the morning were two colonies both of which were watched intermittently from 1:00 a.m. until 8:00 a.m. by which time virtually all activity had ceased. These colonies were getting an abundant supply of booty, partly due to my adding suitable prey to the area in attempting to increase the raiding, and as a consequence these raids may have been unusually long. On one occasion *coecus* was observed raiding between midnight and 2:00 a.m., and on a second occasion another colony was raiding between 8:10 and 8:15 p.m. In both cases the ants could not be found when the areas were searched between 4:00 and 4:30 a.m. the same night.

Nomamyrmex esenbecki (Westwood)

Nomamyrmex esenbecki has been found from southern Texas to northern Argentina, a range almost as great as that of *L. coecus*. Borgmeier considers three subspecific names to be valid: *esenbecki s. str.* (Argentina, Paraguay, French Guiana and Brasil), *crassicornis* (Panamá southward to Amazonas and Pará in Brasil), and *wilsoni* (from Costa Rica northward). Borgmeier (1955: 147) reported that males of *esenbecki s. str.* were taken at the identical locality as males of *crassicornis* but on dates separated by one month. In a later paper he reported that three specimens of *esenbecki s. str.* were taken at the same locality and date as one specimen of *e. crassicornis* (taken in a different year) (Borgmeier, 1958: 201). More collecting may show that these two "subspecies" may be found within the same colony; or, less probably, they may be valid species. There has not been any doubt that all workers and males from Barro Colorado Island belong to the subspecies *crassicornis*.

No bivouac of *esenbecki* has ever been found in spite of the fact that well over 100 colonies have been observed by various workers. In all cases columns of ants disappeared into holes in the ground, and where digging was attempted no bivouac was found. Bivouacs seem to be moved frequently, for the ants are not found in the same area over long periods of time as has been reported for *Labidus*. The best evidence that *esenbecki* may have an activity cycle similar to *hamatum* is that colony E-164 included a contracted queen, a synchronous brood of worker larvae and a brood of callow adult workers on an emigration (discussed below). Schneirla (1957a: 125) reported that three emigrations of *esenbecki* (subspecies?) which he watched for 12 hours or more all included large broods of callow workers, but no other broods were mentioned. Observations on colony E-164 show that the callows of *esenbecki crassicornis* remain much lighter than the older individuals of the colony for at least six days. Since the largest larvae found in this colony were 11.6 mm. long, 0.1 mm. longer than the maximum length for adults, it is clear that the previous brood of adults is still light-colored when a larval brood is full-grown. A single cocoon containing a white *Nomamyrmex* pupa 3.8 mm. long was found in the emigration of colony E-164. Since this pupa is the size of a minim, one would conclude that it must be a rather retarded member of the brood of callow adults. This discovery is the first proof that the worker larvae of *Noma*. *esenbecki* spin cocoons, but it is still not known whether the male and queen larvae make cocoons. The broods of *esenbecki* as well as the entire colonies are estimated to be between three and eight times the size of those of *hamatum* judging from the durations of emigrations.

Raids of Nomamyrmex esenbecki

Borgmeier (1955: 144) lists ten species of ants attacked by *esenbecki*, including *Cephalotes atratus* L. and *Pheidole* sp. which have been seen to defend successfully their nests from species of *Labidus* and *Eciton* on Barro Colorado Island. Workers of *esenbecki* from the locality seemed timid, could not sting my hands and could scarcely bite the skin between my fingers. Therefore, it seems unlikely that such a weak ant could successfully capture the heavily armoured *Cephalotes atratus* which even *E. burchelli* rarely killed. Several estimates of booty found in raid columns of *esenbecki* on Barro Colorado Island indicate that ants are the main food of this army ant, at least 80 to 90% of the booty being immature ants. Schneirla (1957a: 128) also reported that *Nomamyrmex esenbecki* captures soft-bodied "insect brood" and is "competitive to an appreciable extent" with *Eciton hamatum* for food. The preponderance of larvae and pupae in the raid columns in Panamá compared with the records published by Borgmeier of numerous adult ants being carried in columns suggests that the South American *esenbecki s. str.* is a much more aggressive army ant. Also included in the summary by Borgmeier is a report that *esenbecki* was seen to carry off *Eciton dulcius*, but the number of *dulcius* captured and other details were not given. This observation is the only one known to me of *Nomamyrmex* capturing another species of army ant. On Barro Colorado Island *esenbecki crassicornis* was seen to fight a little with workers of *L. coecus* and *L. praedator*, but no army ant carried off any worker of another species. Only on very rare occasions will one species of Ecitonini carry off workers of another army ant. When *esenbecki* (colony E-164) had a raid column touching that of *coecus* (colony E-165), about ten workers of each species traded bites and vibrated antennae at each other for more than four hours. The same individual ants did not persist in this battle for the entire period, but the number of workers stayed relatively constant. Neither species attacked the other army ant as decisively as it attacked other insects near by, and no workers of either army ant appeared to have been injured.

Luederwaldt (1920, quoted by Borgmeier, 1955: 144) reported that *esenbecki* *s. str.* attacked termite colonies and bee hives [= Meliponinae?] in addition to ants. In Panamá *Nomamyrmex esenbecki crassicornis* also avoided attacking many adult insects such as cicadas and beetles the same species of which were readily attacked and cut apart by other army ants such as *Labidus coecus*.

During 1955 and 1956 I observed 17 raid columns from between 14 and 16 colonies of *esenbecki crassicornis* on Barro Colorado Island. These columns were found primarily during the day including 12:30 and 2:50 p.m. in the dry season. It is clear from the data that *esenbecki* does considerable diurnal raiding, but it cannot be reliably determined whether more raiding is done during the night. Colony E-164 was first found at 1:00 a.m. on 18 May 1956 when it had a raid column extending about 15 meters near the west edge of the laboratory clearing. This column was steady and one to three ants wide with occasional myrmecophiles running along it in both directions. The column disappeared about 10:00 a.m. but in the evening it began again, and gradually shifted to an emigration which will be discussed in detail below.

Most of the raid columns observed were weak ones, only one or two ants wide and extending a few meters on the surface of the ground. The ants ran primarily under leaves and other objects making it difficult to find and follow their columns. The workers were observed to enter almost every crack in the ground which they crossed. In most cases the ants came out of these cracks a few centimeters away, but the ends of all columns entered similar cracks and holes with no further epigaeic columns being found near by. On one occasion a column went up a tree and could no longer be seen when it was at least 15 meters from the ground. This column was watched from 9:55 to 11:40 a.m. on 12 February 1956, and it probably continued for at least another hour. Larvae and pupae of ants were the booty recorded being carried down the tree. Such raiding high in trees seems unusual for an army ant which otherwise is so markedly subterranean that its bivouacs have never been found, and epigaeic emigrations are rarely seen. Moreover, this raid occurred on a clear day during the dry season when the preceding week had only 0.01 inch of rain. No raid column of any other colony was seen to go even a few meters up a tree.

Where the distal ends of raid columns could be observed, it was clear that esenbecki is a column raider with only small groups of workers extending the columns and showing no tendency toward formation of a swarm raid. Compared with Eciton spp., Nomamyrmex moves across the ground more slowly, perhaps due to its shorter legs. Dirt tunnels covering raid columns were seen only on one day, 29 June 1956, at 8:00 a.m., when a raid column of colony E-199 was followed for about five meters. About three meters of the trail had been covered by tunnels which were scattered along the route in lengths of 20 to 40 cm. Between sections of tunnel the workers ran along open ground which was as exposed as the areas with tunnels. Since some of the tunnels were on branch columns running in different directions, it is unlikely that these tunnels had been used earlier for an emigration. Bates reported that esenbecki "always" moved under objects and constructed dirt tunnels or arches if it had to move across an open space (1863, v. 2: 364).

Emigrations of Nomamyrmex esenbecki

The major part of one impressive emigration and the probable ends of two others were observed on Barro Colorado Island during 1956. The raid column of colony E-164 had been watched almost constantly from 1:00 to 9:55 a.m.; and although numerous workers and myrmecophiles ran in both directions, all booty was carried toward the old bivouac. The markedly increased traffic about 5:30 a.m. appeared to be the start of an emigration. By 6:30 a.m. the sun was shining brightly on at least three meters of the column, and there was a gradual increase in the amount of ant traffic up to 9:30 a.m. Between 9:30 and 10:00 a.m. the traffic rapidly decreased to nothing. It is possible that the emigration had already begun during this period since part of the colony may not have returned to the old bivouac before the column stopped (due to effects of sunlight?). In the evening of the same day at 6:10 p.m. a raid column two to three ants wide was again bringing in booty along the identical trail, and myrmecophiles were running in both directions along the column. At 7:20 p.m. the first clear sign that the ants would emigrate was that a few pieces of booty were carried in the opposite direction from all booty seen previously. The majority of myrmecophiles were also running away from the bivouac to which the majority of booty was being carried; however, this had been true during the morning also when no emigration had taken place. During the entire period of observation in the morning not a single callow worker had been seen. After 7:00 p.m. a few callows started to appear, and the number of callows increased to about ten per cent near 9:00 p.m. Although more than 60% of the older workers and all the callows were moving toward the new bivouac, by 9:00 p.m. an occasional piece of booty was still being carried back toward the old bivouac. At the same time guard workers began to stand along the edges of the column. These guards were not all the largest workers, but there appeared to be a slight preponderance of larger workers compared with the distribution of sizes running in the column. A light rain between 9:32 and 9:50 p.m. did not interrupt the emigration but may have slowed the ants slightly. The column broadened to three to five ants wide and remained this width until observations ended at 11:30 p.m. By 9:50 p.m. no more booty was seen going toward the old bivouac. Traffic on the emigration column was so dense and rapid that it was almost impossible to collect myrmecophiles without disturbing at least several workers. Most collecting was abandoned to avoid holding up the emigration or perhaps even stopping it. The number of guards increased, and some workers even ran two to five centimeters out from the column for at least the stretch of three meters of trail visible to me from my observation spot. The latter behavior has never been observed along any portion of an *Eciton* emigration route except at the exact places where a disturbance of the column took place. I had not done any collecting along most of this area and probably could not have caused the increase in excitement shown by the ants. By about 10:10 p.m. each row of guard workers along both sides of the column had a density of at least one worker per centimeter. Some of these guard workers were then standing with their front legs off the ground and with their antennae vibrating rapidly. Within the next ten minutes there was a much more pronounced increase in excitement. The number of guard workers at least doubled, and workers were constantly running on the ground outside the row of guards in a direction perpendicular to the column for distances of about five centimeters and then running back to join the guards or the emigrating workers. At 10:21 p.m. a pronounced wave of excitement passed along the column indicating that the queen was probably near. At 10:28 p.m. the queen was spotted moving more slowly than the workers and covered with limulodid beetles. The column did not widen when the queen came along, but the workers accompanying the queen appeared to move faster. Except for a slight increase in speed and an increase in excitement shown by the workers near the queen, no retinue could be distinguished. There had been so much excitement shown by the workers during the preceding 20 minutes that the actual arrival of the queen did not stimulate a great increase in excitement as is often the case with queens of Eciton.

In addition to the brood of callow adult workers, there was a brood of worker larvae ranging in length from 1.2 to 11.6 mm. A small amount of brood was carried just before the queen passed, and the amount increased slightly until 11:30 p.m. when observations were temporarily ended.

For one-half hour during the remainder of the night it rained a total of 0.27 inch which may have interrupted the column for a few minutes. At 7:00 a.m. the following morning (19 May) the emigration was still in progress. The only differences noted from the previous night at 11:30 p.m. were: (1) the number of guard workers had decreased slightly (but these still lined the route almost continuously on both sides); (2) the rows of guard workers were slightly closer together making a passageway 1.0 to 1.5 cm. wide; and (3) the moving column was only one to two ants wide; and (4) the traffic toward the new bivouac consisted of over 95% callows. The guard workers, as during the previous night, were all dark ants contrasting greatly in color with the band of light workers between the rows. In some places the guards straddled the column with their legs, and some guards stood on top of others forming a tunnel of workers. More than 95% of the guard workers at this time were facing in toward the center of the column. The percentage facing inward during the night before had been considerably less, but no record was made. In the morning a branch column one meter in length came out of the ground about one meter from the main column and joined it. Along this column guard workers were present but not as numerous.

Larvae were being carried exclusively by dark workers which also carried an occasional callow. The majority of brood must have been transported during the night when observations were interrupted. However, thousands of larvae were still carried between 7:00 and 11:00 a.m. Observations were not made continuously during this period while the column was gradually decreasing in strength. By 11:40 a.m. between 10% and 30% of the ants running toward the new bivouac were callows. The proportion of ants returning toward the old bivouac had increased to 30% of the total traffic, and the returning ants were still all dark individuals. Some of these may have been starting to backtrack because the queen had been removed from the emigration column. Guard workers were still scattered along the column every few centimeters, and a few myrmecophiles were running along the column toward the new bivouac.

The emigration was still progressing at 2:30 p.m. on 19 May, but no guard workers were present, and the column was a single ant wide. Dark workers were running in both directions in approximately equal numbers, but callows and myrmecophiles were still seen running only toward the new bivouac. However, between 2:30 and 3:00 p.m. 15 callow and four dark workers were seen being carried by old workers, and in the same period only nine callows were seen running. Earlier the proportion of callows seen being carried was much less. A similar increase in callow and dark workers being carried has been noted at the end of emigrations of E. burchelli and other species. By 4:45 p.m. the emigration was considered terminated since only one dark worker was seen every 20 to 30 cm. along the trail. At 7:00 p.m. the trail was visited again, and the backtracking column included callow and dark workers going in both directions. Later in the evening a raid column was seen near by which undoubtedly came from the new bivouac, and the backtracking column apparently continued with little interruption for at least four days.

The majority of traffic on the backtracking column went along the branch trail mentioned earlier. This trail is not the one over which the queen had emigrated indicating that the ants do not stop backtracking at the point where the queen is taken and do not restrict their backtracking to routes over which the queen has passed. Throughout the period of about four days, when backtracking was observed, the ants gradually deviated more and more from the route used on the emigration. On 22 May both dark and callow workers were carrying larval brood in both directions along the backtracking column. The callows were only slightly darker in color than those seen on the emigration on 18 May.

The end of another emigration (colony E-160) was watched from 8:10 to 8:20 a.m. on 14 May 1956. Four workers ran into the hole in the ground between 8:20 and 8:35 a.m., and myrmecophiles continued to run along the trail until 8:55 a.m. A raid column came out of the same hole into which the ants were emigrating throughout the period from 8:10 to 10:00 a.m. The raid column was easily distinguished from the emigration column by the booty being carried toward the hole, by the traffic being approximately equal in both directions, and by the much smaller number of myrmecophiles in the raid column. On 18 July 1956 the end of a probable emigration column was also observed from 11:25 to 11:30 a.m. (colony E-215).

Interrelations Among Individuals of Nomamyrmex esenbecki

When workers were released into the dish with queen E-164, the workers ran around the dish and over the queen in an excited manner for about one minute. Then the workers rode on the gaster of the queen or stood with their heads over the queen without licking her. When the queen ran around the dish the workers followed. A total of 14 workers was added to the dish, but within 36 hours eight were dead or so weak that they could no longer keep up with the queen when she walked quickly. Workers rode only on the gaster of the queen, but even active workers had difficulty staying on the gaster when the queen was running. Table 2 summarizes a record kept of the abdominal segments near which the workers held their heads when standing on or next to the queen. The totals are far different from those recorded for a queen of _hamatum_. Although, compared with _hamatum_, many more of the workers seemed to be attracted to the segments behind the first gaster segment, there was no attraction to the genital opening or anus of the queen. Workers were attracted to the lateral and ventrolateral areas of the second, third and fourth gaster segments, but not to these areas of the fifth. Workers were seen to lick the head, thorax, fifth gaster segment, one front leg and an antenna of the queen. Much more cleaning or licking of this queen was observed than for a comparable period of observation of any of the _Eciton_ queens. At least twelve limulodids were almost constantly riding on the queen. These beetles licked the queen much more than they licked any of the workers and much more than the workers licked the queen. At no time did the workers attack the beetles on the queen.

Most workers of esenbecki crassicornis died in the laboratory within 24 hours after they were collected. A small number of workers of E-164 kept in a petri dish with their queen, booty from their emigration and water were dead or dying within two days. The queen remained active and not only walked around the dish but attempted to climb the sides several times. The queen never paused to drink or feed at the water-soaked cotton or booty in the dish. However, when a small wad of wet cotton was held up to her mouthparts with forceps, she spread her mandibles and drank some of the water. She also licked a piece of ant pupa which was broken open and held in front of her. Like the workers, the queen vibrated her antennae constantly as she walked, and the recurved distal portions of the flagella touched the floor of the dish. The queen was placed in Bouin's fixative when she was still active on 20 May 1956 at 5:00 p.m. A description of this queen has been published by Borgmeier (1958a).

Flight Dates for Males of Nomamyrmex esenbecki

Borgmeier (1955: 150) records a male taken in April 1930 at Balboa, Canal Zone, and one taken in May 1946 at Barro Colorado Island. Additional records for males found at lights on Barro Colorado Island during 1956 are as follows (with the number of males in parentheses): 22 May (1); 5 June, 2:30 to 3:00 a.m. (12, including one which lost wings when taken); 6 June, 5:15 a.m. (8, including 4 which lost wings immediately); 16 June, 4:30 to 5:30 a.m. (1); 17 June, 5:00 to 6:00 a.m. (3). Several of the males were seen flying from the forest to the lights on 5 June and

6 June, and it may be significant that these males were all taken between 2:30 and 6:00 a.m.

Nomamyrmex hartigi (Westwood)

Nomamyrmex hartigi ranges from Paraguay northward to Panamá where it is known from both the Atlantic and Pacific sides of the isthmus in the region of the Canal Zone. The species has not yet been found on Barro Colorado Island, but some specimens were sent to me by Wilford J. Hanson who found them in the Canal Zone at Cerro Galera, K-6 road, on 19 January 1959. Of particular interest are his observations that the ants were raiding termites and going up the tunnel made by the termites on the side of a tree. When the tunnel was broken the ants formed bridges and walls in the gaps. Borgmeier (1955: 159) reported that Schwarzmaier observed hartigi raiding termites and Atta in Goiás, Brasil.

Neivamyrmex pilosus (F. Smith)

Neivamyrmex pilosus, which has been found from Texas and Arizona to northern Argentina, has a wider range than any other species of Neivamyrmex; in some localities it is the most abundant species of army ant. On Barro Colorado Island pilosus is relatively rare but is the most commonly seen species of the genus. During 1956 we found columns of eight colonies compared with a total of four colonies of three other species of Neivamyrmex. Borgmeier (1955: 372-375) has included five subspecies within pilosus, but these can be distinguished only on the basis of males. The queen has been found for one subspecies. The subspecies mexicanus (F. Smith) has been found from Texas to Panamá, including Barro Colorado Island.

Bivouacs of pilosus are subterranean or within logs, but no bivouac has been described. Eidmann (1936: 32) reported that the larvae seen in an emigration were all of the same approximate age, and thus he concluded there must be a regular reproductive cycle. We found larvae ranging in size from 2.4 to 4.8 mm. in an emigration column (colony E-227) on Barro Colorado Island. This evidence for synchronous broods and the lack of reports of permanent or semipermanent bivouacs support the hypothesis that pilosus may have regular nomadic and statary phases. The two queens which have been found were both contracted and taken in columns (Borgmeier, 1955: 283; Schneirla and Brown, 1950: 325).

Raids of Neivamyrmex pilosus

It is clear from observations on Barro Colorado Island, as well as from the literature summarized by Borgmeier (1955: 366-369), that pilosus has column raids. The largest, most active raid columns had distal groups of advancing workers forming miniature swarms ten to 40 cm. wide. Most columns had much smaller advancing groups which moved solely in narrow columns. Ants carrying booty along raid columns were seen to disappear into holes in the ground in several places a few meters apart. However, there was no indication that these holes were abandoned and others used during the course of the raid as happens frequently with Labidus praedator. There were two characteristics of the raid columns which distinguished them from those of other Ecitonini seen on Barro Colorado Island; (1) at times almost all of the workers were carrying booty, and all the ants were running in the same direction, and (2) the workers came along the columns in spurts or in groups with gaps between the groups where there were few or no workers for one to several meters.

One of these surges of ants changes the column suddenly from a few scattered workers to a tightly massed group two to five ants wide extending for five or more meters. Although fluctuations in traffic are common along columns of all army ants, these changes appeared to be much more distinct with pilosus. Nevermann also observed the ants running in the same direction and found that emigrations ended quickly without any stragglers (reported by Reichensperger, 1939c: 300).

On Barro Colorado Island all colonies were found between 14 May and 5 August 1956, indicating that the species does not raid frequently if at all on the surface of the ground during the dry season. Three raids were found between 1:00 and 6:00 a.m., and five were found between 10:00 a.m. and 2:00 p.m. One colony had an active raid on 28 May 1956 between 1:25 and 1:45 p.m. which would be during the siesta period for Eciton spp. All booty seen indicates that pilosus feeds almost exclusively on species of ants the same size as itself or somewhat smaller, and captures adults, larvae and cocoons. A preference for Crematogaster reported by Borgmeier (1955: 367) was further substantiated by booty in several columns. The workers were also seen carrying a small spider, but they were not attracted to peanuts placed beside their columns. This species of Neivamyrmex has a more severe sting and bite than many of the larger army ants such as E. hamatum and dulcius.

Emigrations of Neivamyrmex pilosus

On 17 May 1956 a raid column (colony E-163) had been watched between 6:45 and 7:00 a.m. as the raid was ending. The following day at 1:00 a.m. no ants could be found along the route of this column or near by, but by 1:45 a.m. there was a strong raid column. About 4:00 a.m. this raid column shifted to an emigration, judging from the reversal of the direction in which booty was being carried. However, between 6:30 and 7:00 a.m. the emigration abruptly ceased before any brood, myrmecophiles, or the queen had been seen. No column was seen again in this locality even though the area was searched several times during the following night. An emigration column of a second colony was watched from 9:50 to 11:00 a.m. with similar results.

Flight Dates for Males of Neivamyrmex pilosus

Males were taken at lights on Barro Colorado Island on the following dates (with the number of males in parentheses): 30 March 1952, about 1:00 a.m. (1); 1 April 1952, 10:00 to 11:59 p.m. (5); 25 March 1955 (1); 28 March 1955 (2); 29 March 1955 (1); 18 April 1956 (1); 19 April 1956, 12:30 to 2:00 a.m. (2); 21 April 1956 (1); 28 April 1956 (7); 3 May 1956, 2:00 a.m. (1), 4:30 to 5:00 a.m. (5); 8 May 1956, 9:30 p.m. (1); 9 May 1956 (1); 10 May 1956, 9:00 p.m. (1); 11 May 1956 (1); 12 May 1956, 5:00 a.m. (1); 16 May 1956, 6:45 a.m. (4); 18 May 1956, 4:00 a.m. (4). The above 40 males were taken between 25 March and 18 May, and Borgmeier lists five additional records for males taken within these dates in Panamá and Costa Rica. In México and the southern United States the flight dates are later, ranging from 30 May to August (Borgmeier, 1955: 374).

Neivamyrmex gibbatus Borgmeier

Neivamyrmex gibbatus is a fairly common species known from Costa Rica, Panamá and British Guiana. The male is unknown, but a contracted queen was taken by R. Z. Brown from an emigration column on 19 January

1948 at 11:00 p.m. (Schneirla, 1958a: 219). During 1956 I found two colonies raiding at night during the rainy season. The first (colony E-158) was watched from 3:25 to 4:35 a.m. on 3 May, when it had one strong raid column three to five ants broad extending southward from a hole in the ground. In addition, two weaker columns went toward the north and northwest. When the main column was visited again at 5:50 a.m., it had decreased to a column one ant broad, and the other two columns had vanished. This column was followed for about 25 meters on the surface of the ground until it disappeared down two or more holes. Much booty consisting of larval, pupal and adult ants was being carried; and if the column was disturbed, the workers carrying booty would stream in opposite directions along the trail. Other workers rushed out from the trail at the point of disturbance. All workers could give a painful sting without any lasting effect, but their bites were ineffectual except on tender skin. The workers appeared to be disturbed by light to the same extent as those of Eciton burchelli.

A second colony (E-241) was found raiding at 9:25 to 9:50 p.m. on 7 August 1956. This raid column was ten ants wide, which is exceptionally wide for a raid column of any species of army ant. In spite of the large numbers of ants along the column, there was no swarm at the distal end of the column. The main column branched, and the advancing ants stayed in narrow columns or fanned out to form miniature swarms 20 to 30 cm. wide. All booty collected from this raid column consisted of immature and adult ants of several species. On the following day at 7:15 to 7:25 p.m. there was a raid column in the same locality. At the ends of several raid columns when the workers were withdrawing from the area, there were no, or at most only one or two, workers running back in the opposite direction from the retreating ants. The only stragglers seen were two injured workers and two probably myrmecophilous Thysanura.

At one point the raid column of E-241 touched a raid column of *Eciton dulcius crassinode* (colony E-242). The two species avoided each other without fighting, possibly because both columns were a single ant wide and not raiding vigorously.

Neivamyrmex humilis (Borgmeier)

Neivamyrmex humilis previously had been known from a single locality, San José, Costa Rica. It must be a relatively common species there since H. Schmidt found a number of colonies and seven queens. He also found 15 males, nine dark male pupae apparently ready to emerge and some workers in a raid column of *Eciton vagans*. Presumably the *humilis* had been captured by the *vagans*, but no further information was given (Borgmeier, 1948a: 197). The time of year when males of *humilis* are produced is still unknown.

This small orange army ant was found raiding between 11:00 and 11:30 p.m. on 26 July 1956 in the laboratory clearing on Barro Colorado Island. The raid column extended a maximum of six meters from a hole in the ground and had at least four branches. One branch went about 30 cm. up the side of the laboratory where the army ants were raiding an ant colony. A staphylinid larva was taken as it was running along in the midst of the army ants. No other myrmecophiles were seen, but a diapriid was later found among the aspirated ants. The ants were carrying one small spider, one immature homopteran, some adult ants and numerous larvae and pupae of ants.

Bright white light did not disturb the raid column as much as it does columns of other species of army ants, but aspirating ants caused workers along the column to rear up in the typical position of army ants when highly excited. Similar behavior resulted when a small, partially crushed cricket (Gryllidae) was dropped on the raid column. The cricket was still moving, but the ants would not attack it. The workers made a ring around the cricket with all the ants facing it. Occasionally one worker would rush toward the cricket until the ant's antennae touched the gryllid, and then the ant would rapidly run backwards. The raid column made a detour around the cricket, and no worker attacked it. The *humilis* workers seemed unable to sting my hands, and their bite was weak.

Neivamyrmex postcarinatus Borgmeier

Neivamyrmex postcarinatus is known only from Barro Colorado Island. Previous reports are limited to the type series collected by Schneirla on four dates: 21 February 1946, 8 March 1946, 18 March 1946 and 16 January 1948. On 1 February 1955 I watched one raid column from 9:45 to 10:00 p.m. It is of interest that all five records fall between 16 January and 18 March during the beginning and middle of the dry season. The raid column which I observed followed the buttress root of a huge tree for at least eight meters, and this same route had been used by both *Eciton burchelli* and *E. hamatum* colonies within the preceding two days.

Neivamyrmex opacithorax (Emery)

Neivamyrmex opacithorax has a range approximately equivalent to that of *Neiv. nigrescens* in the United States, and in addition the former species extends southward to Costa Rica. Both species are found throughout most of the southern states from California to North Carolina and extend farther north in the plains states, Kansas, Nebraska and Iowa (M. R. Smith, 1942: 558; Borgmeier, 1955: 504).

There are a number of seemingly contradictory statements in the literature regarding the relative abundance of these two species. Cole (1953b: 84) reported that *opacithorax* was much more common in New Mexico than *nigrescens*. In the Gulf States, M. R. Smith (1942: 560) reported that *opacithorax* is "never so abundant as" *nigrescens*. Schneirla (1958a: 221) reported that in Arizona *opacithorax* is "perhaps as common" as *nigrescens*, but he also stated, "more than 12 colonies of *Neiv. nigrescens* and 6 colonies of *opacithorax* were found...." (p. 241). Part of the above discrepancies may be explained by the report that *nigrescens* is more abundant in the southeastern United States compared with farther west (Creighton, 1950: 65). Perhaps of more importance are the precise habitats of the two species. In Kansas, *opacithorax* has been found in open fields, and in park-like areas within cities. *Neiv. nigrescens*, on the other hand, has not been found in these areas but was found within more moist wooded areas. Although this conclusion has been based on a total of only about 15 colonies of the two species found in Kansas, it suggests that *opacithorax* may be restricted to drier areas throughout the country.

Raids of Neivamyrmex opacithorax

Neivamyrmex opacithorax appears to feed almost exclusively on ants and carabid beetles. The capturing of larval and adult Carabidae seems to be a common occurrence since three colonies of *opacithorax* in Kansas had killed numerous specimens, and Wheeler and Long (1901: 163) reported that opacithorax in Texas had captured "a considerable number of small carabid beetles." Ants probably are more frequently killed in all localities, and ant larvae taken from raid columns showed no movement, probably indicating that they are killed by stings of the army ants at the time of capture. Workers from three colonies showed little attraction toward pecans, English walnuts or roasted peanuts, but two workers at one time chewed on a piece of walnut for about five seconds.

Raids of *opacithorax* primarily occur in the evening, night and early morning. On cloudy days raids may be extended throughout the day, but the ants rarely raid in sunlight. In all cases the raids seen were column raids with no tendency toward swarm raids. On several but not all raid columns each incoming ant carried a piece of booty. It appears that *opacithorax* may be more efficient than the common species of *Eciton* in that fewer *opacithorax* workers return without prey. It is uncommon to see two or more workers of *opacithorax* carrying a single piece of booty, whereas such tandem carriers are frequent among *Eciton* spp. The column raids of *opacithorax* look inefficient at capturing prey since the ants do not run up low vegetation including even short blades of grass. Numerous insects retreat a few centimeters up on objects and completely escape the ants. The raid columns often show greater fluctuations in traffic than those of most army ants observed, but the fluctuations are not as great as those seen along raid columns of *Neiv*. *pilosus*.

Some additional information on the raiding of this species is given by Schneirla (1958a).

Emigrations of Neivamyrmex opacithorax

Three emigrations of opacithorax have been seen in Lawrence, Kansas. The first one found occurred on 3 June 1958 starting probably about 10:00 p.m. When the colony was first visited at 10:25 p.m. that night, there were no raid columns, and a steady emigration column extended from one hole in the ground to a second hole under a dense bush 50 cm. away. The exact location of the subterranean bivouac(s) is unknown, but since 26 May the ants had raided daily coming out of one or more of five holes within a radius of 16 cm. If one considers 26 May as the first statary day, the ants were emigrating on the ninth statary day or approximately the middle of the statary phase. From 10:25 until 11:10 p.m. the emigration column increased in width slightly until it was between three and five ants wide. No callows were seen in the column, and the brood being carried was in the egg stage. By 11:35 p.m. guard workers had positioned themselves along the column. Some of these became quite excited partly due to my collecting. In addition, a lycosid spider walked across the column, and a sowbug and a caterpillar started to walk across and retreated. The caterpillar was severely attacked; however, the other arthropods were not injured. The excited guard workers sometimes climbed as high as two centimeters up on vegetation, and sometimes ran about six centimeters out from the emigration column. At six minutes past midnight the physogastric queen came walking along the column. The column was highly aroused by that time, and there was no discernible wave of excitement due to the advance of the queen. It is possible that the queen had some difficulty getting through the hole in the ground which was just large enough for her to pass. A solid row of guard workers was along 50 cm. of the epigaeic route, but these guard workers were not arranged in a compact wall or tunnel as has been observed with L. praedator and other army ants. The queen had about six workers on her in the emigration column, but these were riding and in no way helping her progress along the column. In spite of appearing to be in a maximally physogastric condition, the queen had no obvious difficulty running along the column. The workers of opacithorax, like those of other species of army ants, can run appreciably faster than the queen on a level surface. Most of the egg brood was carried before the queen was seen, but additional brood was carried up until about 12:28 a.m. By this time the number of guard workers had markedly decreased in number, but the width of the column remained approximately the same. By 12:34 a.m. all the guard workers had left, and occasionally a packet of eggs was carried by. Before the queen emigrated, one could see more than 25 packets of eggs along a stretch of column 30 cm. long, but by 12:34 a.m. a maximum of one packet per 30 cm. could be found. Between 12:40 and 12:51 a.m. the column got abruptly thinner, more ants seemed to hesitate and go back along the column a few centimeters, and the first two workers were seen being carried. Several ants were seen to walk more or less sideways, hesitating and picking up dirt and pieces of wood. These workers appeared to be a clean-up squad checking to see whether anything had been left behind. The behavior, which is not seen along the emigration column when it is thronged with actively moving ants, probably is responsible for the carrying of workers and guests more at the end of emigrations rather than during the beginning and middle periods. At 12:54 a.m. the last ants had passed. The end of this emigration made slow progress since the ants ran back along the column and also constantly ran five to ten centimeters laterally from the trail. The caterpillar which had been attacked about 11:40 p.m. was gradually abandoned during the last half hour of the emigration. It struggled constantly while the ants were attacking it and was unable to crawl when abandoned. Observations continued along the trail until 1:31 a.m.; and although no further ants passed, a few phorids and staphylinids were seen.

In addition to the large number of eggs seen being carried on the emigration, the queen from the above colony laid about 9,500 eggs after she was taken. As far as could be determined she did not eat during this period. (More details of the oviposition are given below in the section Oviposition and Queens of *Neivamyrmex opacithorax*.) The exact location of neither bivouac is known; but since the epigaeic emigration column was just 50 cm. long, it is highly probable that this was not a normal emigration. Similar short "emigrations" or bivouac shifts of *E. hamatum* and *burchelli* have been seen during the statary phase. However, the bivouacs of these two tropical species had been disturbed, and the bivouac sites in some cases had been completely destroyed. There was no known disturbance of the bivouac of this colony of *opacithorax*. The holes used by the ants were at the edge of a driveway, and it is possible that the bivouac was under the driveway and in too hot and dry a location for the ants.

Not a single callow worker, pupa or larva was seen in the emigration. Although Schneirla (1958a) has given good evidence to support the hypothesis that *Neiv. nigrescens* has a nomadic-statary cycle homologous to *E. hamatum*, there is no comparable evidence for *Neiv. opacithorax*. This emigration of colony E-163 was undoubtedly atypical since it occurred in the middle of the oviposition period. At that time one would expect a brood of pupae to be present, and perhaps the absence of this older brood was partially responsible for the unusual emigration. (It is unlikely that an entire pupal brood would have emigrated by a subterranean route or remained in a subterranean bivouac while the rest of the colony emigrated on the surface.) It is highly improbable that the egg brood was the first brood of the year since opacithorax is active on the surface (but may not have broods) in Lawrence, Kansas, at least as early as 10 April.

On the evening of 4 June about 18 hours after the queen was taken there was no backtracking column at 6:20 p.m.; however, at 10:15 p.m. a column was going toward the old bivouac site but into a hole about 18 cm. closer to the new bivouac than the exit hole used on the emigration. Thus, the ants were not backtracking along the trail actually used on the emigration but were using a different route of an earlier raid column. A few workers occasionally stuck their heads out of the exit hole used on the emigration, but no workers formed a connecting column on the surface of the ground. Two workers which had been kept in the laboratory with the queen were placed along the backtracking column. There was an immediate wave of excitement followed by an increase in the number of workers along the column. On 5 June a backtracking column was still present, and no further observations were made.

Another emigration (colony E-264) was watched on 6 July 1959 on the campus of The University of Kansas. A raid column had been seen crossing a sidewalk next to Snow Hall during the day at 11:30 a.m. and 12:40 p.m. At these times the ants were going out on the column at a rate of about 50 ants in one minute and six seconds. Less than ten per cent of the number of ants going out were returning. By 7:15 p.m. the column had increased to 50 ants going out in ten to 20 seconds with less than five ants going toward the bivouac in the same interval. By 8:45 p.m. traffic was more steady at about 50 ants going out and nearly 12 going in during 12 seconds. Booty was first seen being carried out at 8:53 p.m., and by 8:56 p.m. larval brood was carried. At this time approximately two per cent of the ants carried either booty or brood. However, at 9:02 p.m. the amount of brood increased markedly until about 50% of the workers were carrying brood, and the traffic had increased to its maximum of about 50 ants going out in five seconds. At 11:22 p.m. the ants became more excited, workers ran one to five centimeters away from the column along both sides, and many more workers ran back toward the old bivouac. The queen was taken at 11:41 p.m. Up until 1:35 a.m. on 7 July when observations were ended, the number of ants going toward the new bivouac remained at the maximal rate, and workers went back toward the old bivouac at about 25% of the outward rate. Many callows and a few minor worker pupae were seen in the emigration. Only dark workers were seen returning toward the old bivouac and carrying other workers.

A strong backtracking column was found along the emigration trail between 10:00 a.m. and 1:00 p.m. on 7 July. The column consisted solely of dark workers running in both directions in approximately equal numbers. At 8:00 and 9:00 p.m. the traffic on the backtracking column was the same or slightly stronger. At 7:45 a.m. the following morning the traffic on the column had decreased from its previous strength at night, and the first callow was seen in the column. The column continued throughout the day, and the first brood or booty was seen being carried toward the old bivouac (of 6 July) at 7:00 p.m. The backtracking column persisted until 10 July when it was noticeably weaker at 10:00 a.m. compared to previous days at that time. On 10 July at 6:00 p.m. and the entire following day there were no longer any ants along the trail.

A third emigration (colony E-266) was watched almost continuously from 9:00 p.m. to 3:20 a.m. on 19 to 20 August 1959. Throughout this period numerous callows were seen, and booty and a brood of worker larvae about three-fourths grown were being carried. The queen was not seen, and neither guard workers nor greatly excited running workers were seen, indicating that she probably had not emigrated before 3:20 a.m. On 20 August at 7:30 p.m. there was a weak column of about one ant per ten centimeters (including the approximately equal traffic in both directions). This column had disappeared by the following morning, and it is impossible to determine whether it was a backtracking column (possibly followed by a continuation of the emigration) or a raid column. Similar columns along previous emigration routes have also been reported for <u>nigrescens</u> (Schneirla, 1958a), but such columns are not found or are rare among <u>Eciton</u> spp.

Bivouacs of Neivamyrmex opacithorax

All bivouacs of <u>opacithorax</u> which have been located were subterranean, and their exact positions and sizes are unknown. On five occasions in the vicinity of Lawrence, Kansas, clusters of <u>opacithorax</u> have been found under small stones. Each of these clusters was considered to be less than five per cent of the total colony. Similar "bivouacs" under stones mentioned by Schneirla (1958a) probably were not entire colonies. Brood was never found in any of the clusters in Kansas except for the adult males in colony E-267 discussed below. However, <u>opacithorax</u> like <u>nigrescens</u> probably brings at least part of its brood up from more subterranean bivouacs to areas under stones on the surface of the ground. These stones were all exposed to bright sunlight during the day, and an unusually high number of staphylinid beetles or mounds of loose dirt indicated that the ants had been much more numerous under each stone than they were at the time they were found.

Oviposition and Queens of Neivamyrmex opacithorax

The queen from colony E-263 in the laboratory laid 9,500 eggs within 42 hours of the time when she was taken from an emigration column. This rate of oviposition is 226 per hour or 3.8 per minute. Judging from the few colonies which I have seen, the colonies and broods of *opacithorax* and *nigrescens* are essentially the same size. At the above oviposition rate it would take the queen almost seven days to lay a brood of 37,000 eggs. A brood of that size was considered to be average for *Neiv. nigrescens* (Schneirla, 1958a: 242-243). However, it is known from observations on physogastric *Eciton* queens that when these queens are brought into the laboratory, they cease laying sooner than if left with their colonies. In addition, *Eciton* and *Neivamyrmex* queens become noticeably weak and often die within a few days in the laboratory. As a consequence the oviposition rate in a normal bivouac may be considerably higher. Records for the first 19 hours indicate that queen E-263 laid at a rate close to 300 per hour which is probably closer to the rate in a bivouac. At this rate she could have laid a brood of 36,000 eggs in five days.

Actual egg laying occurred in irregular spurts with sometimes more than five minutes between two groups of eggs. The eggs most frequently were laid in groups of two to eight eggs stuck together at their tips.

Five or six eggs usually were laid in 30 seconds. The eggs appeared moist when laid and readily stuck together in packets without licking or handling by the workers. The queen often rested partially on her side when ovipositing and frequently walked around the dish scattering eggs wherever she went. The workers gathered up most of the eggs and placed them in piles. Several workers ate some eggs while turning their abdomens under as if they were stinging the eggs at the same time. It is not known whether the workers also eat eggs or other brood in a bivouac, but it is a well-known fact that other Ecitonini eat their brood of all ages more readily in the laboratory than under field conditions.

The queen was kept alive until 6:00 p.m. on 5 June 1958 when she was placed in Bouin's fixative. No eggs had been laid during the preceding hour, and only a few were laid in the last three hours before preserving the queen. As far as we could determine the queen did not eat nor drink anything while she was in the laboratory. The queen from colony D-175 taken by Howell V. Daly from a cluster under a stone also was never seen to feed, but the workers with her readily drank water and fed on a partially crushed housefly. This queen was observed to clean her own antennae with her front legs, but no queen of Neivamyrmex, Nomamyrmex nor Eciton was observed to clean any part of her body. All queens of Ecitonini usually ran around with their mandibles spread, but they would never bite anything even if an object was placed between the mandibles.

Sexual Broods of Neivamyrmex opacithorax

Colony E-267 was found about 2:00 p.m. on 21 October 1959 by people who complained that their home was being invaded by insects coming up between floor boards. Investigation on the following day at 10:00 a.m.

showed that the colony had a brood of alate males which were entering the house along with some workers, and additional males were at the edges of the foundation on opposite sides of the house. Workers were more numerous along the inside edges of the foundation where small clusters of up to 200 workers were scattered for more than a meter along the rough field stone foundation. No brood other than the adult males could be found, and the largest part of the colony (or colonies) must have been under the foundation. Most of the males had a number of workers clinging to them. The two groups of ants were about six meters apart with no ants seen between the opposite sides of the house externally or in the crawl space under the house. These two groups may have been daughter colonies following a colony division.

A total of 52 males was taken and 27 of these were kept alive in a laboratory nest. When placed in this nest at 1:00 p.m. on 22 October, three of these 27 males ran around the nest, tried to fly and were attracted toward a microscope light. Several males clustered with workers on a petri dish filled with moist cotton. Most of the males clearly moved away from the light and slowly walked until they reached the darker corners of the nest. These latter males neither fanned their wings nor flew when dropped. Most of the males had died by the morning of 24 October. The workers pulled the dead males around the laboratory nest a little but did not eat any part of the males nor do any damage to them.

A circular column was found on 25 October at 2:00 p.m. after the males had all died. This column, shown in figure 1, continued for over six hours without any interruption even though the cover of the nest was removed and lights were turned on and off repeatedly.

Published records for males of *opacithorax* indicate that this species has males in September and October throughout the northern part of its range (M. R. Smith, 1942: 558; Borgmeier, 1955: 504). The earliest and latest known collection dates for males of *opacithorax* in Lawrence, Kansas, are "September" and 22 October based on specimens in my collection taken during 1945, 1956, 1959 and 1960. In Florida males have been taken on 10 November 1911 (M. R. Smith, *l. c.*), 9 December 1948 (Borgmeier, *l. c.*); and I found one alate male on 9 February 1956 at 2:00 p.m. along the tide line at Crandon Beach Park, Miami. The latter male was soaked but still alive and probably had been washed up on the beach after falling into the water a few feet offshore. Records from Georgia to Arizona fall between August and November, and one record for Costa Rica is for April (M. R. Smith; Borgmeier, *l. c.*).

Neivamyrmex nigrescens (Cresson)

Neivamyrmex nigrescens has been found from the southern United States to Guerrero, México. As discussed above under *Neiv. opacithorax*, the distribution of *nigrescens* may be primarily in the more moist and wooded areas of the region. The fact that about half as many colonies of *nigrescens* as *opacithorax* have been found in the vicinity of Lawrence, Kansas, is attributed to *nigrescens* being absent or more rare in clearings or within the city. Males of *nigrescens* have been found during the same period as those of *opacithorax* in the United States. However, I have never found any male *nigrescens* in Kansas, and their much greater scarcity probably indicates that colonies of *nigrescens* are less abundant than those of *opacithorax*. Unlike males of the epigaeic species of *Eciton* which fly from emigration columns, the males of *nigrescens* were observed flying from a nest near Austin, Texas (Wheeler, 1910: 263).

Raids of Neivamyrmex nigrescens

Neiv. nigrescens has column raids similar to those of *opacithorax*, but it appears to feed primarily on ants and less frequently captures beetles. The following foods were put in a laboratory nest containing about 1,000 workers of *nigrescens*: peanuts, cashew, hazel, English walnut, and black walnut nutmeats, raisins, dried coconut, sugar syrup (sucrose), peanut oil, margarine, butter, bacon grease and ground beef. As far as could be determined, not a single ant ate any of these substances. During the same period the workers were seen to drink water and eat one collembolan and some of their pupal brood. In spite of the large number of pupae which remained alive in the nest, most of the workers died within seven days, and all were dead within 11 days. Since *Eciton hamatum* and *burchelli* readily eat their brood, one would expect that *nigrescens* would have eaten a much larger proportion of the pupae. For further details on the raids of *nigrescens* one should consult the paper by Schneirla (1958a) which is the most thorough study made on the raiding of any species of *Neivamyrmex*.

Emigrations of Neivamyrmex nigrescens

The most extensive observations on emigrations of *Neivamyrmex* have been made by Schneirla (1958a) who studied over 60 emigrations of *nigrescens* in Arizona. The general pattern of the emigrations appears to be comparable to that of *E. hamatum* except that the queen "usually makes her journey at some time after the emigration is roughly one-third completed" (Schneirla, 1958a: 245). This statement suggests that the queen leaves the old bivouac much earlier than those of Eciton, and perhaps this is correlated with a high position of the queen in the subterranean bivouacs where she is close to the surface of the ground. In addition, emigrations frequently may be started on one night and continued on the following night.

Unlike the typical nomadic phases of Eciton hamatum in which colonies emigrate nightly with rare exceptions, it is common for a colony of nigrescens not to emigrate on one or several nights during the nomadic phase. A comparison of figures 73 and 74 based on data published by Schneirla will readily indicate the greater number of nights throughout the nomadic phase when colonies of nigrescens did not move. These data are not sufficient to show any clear pattern. However, as pointed out by Schneirla (1958a: 250), there is the greatest tendency to omit an emigration on the day following the first emigration of the nomadic phase. These data indicate that there is no clear increase in the distance that a colony emigrates during the course of the nomadic phase. One might expect that a colony would have larger raids and would emigrate a greater distance near the end of the nomadic phase, based on the hypothesis of Schneirla that the stimulation of the workers by the larvae increases as the larvae increase in age. Not only is there no clear increase in the distance, but there are three records for colonies which did not emigrate at all on the day preceding the last nomadic day. Although Schneirla seems to imply that the first nomadic emigration is especially "vigorous," figure 74 indicates that the colonies do not necessarily emigrate a greater distance on this emigration than on any of the others.

Bivouacs of Neivamyrmex nigrescens

All bivouacs of Neiv. nigrescens are subterranean, and although typical nests probably extend at least one meter below the surface, two bivouacs found near Lawrence, Kansas, were largely or completely within the upper 30 cm. of soil. Colony E-101 was first found by Dr. Henry S. Fitch at The University of Kansas Natural History Reservation on 28 June 1955 at 9:00 a.m. At that time a mass of workers and brood 15 to 20 cm. in diameter was found under a stone. On the following day at 2:00 p.m. approximately one tenth as many workers and a little brood were found under the same stone. When the ants were visited again at 9:30 a.m. the subsequent day (30 June), the mass was about 13 by 18 cm. in size. The stone was in bright sunlight most of the day in an area of scattered trees and shrubs next to a more dense woodland. These meager data suggest that the ants bring their larvae near the surface during the afternoon and evening and carry them deeper in the middle of the day if the rock becomes too hot. The brood consisted of worker larvae which were starting to pupate, but since Neivamyrmex spp. do not spin cocoons, the shift in larvae was not identical to the movement to spinning areas found in Eciton colonies during this period. Schneirla (1958a: 250) concluded that the "statary condition did not ensue in the colonies until the naked brood entered the early pupal stage." However, colony E-101 clearly became statary before any, or at most less than one fourth, of the larvae had transformed to pupae. Thus Schneirla's hypothesis (that the nomadic phase is terminated largely because of the cessation of stimulation by the larvae) is substantiated better by this case than by his records from Arizona. (Perhaps Schneirla's use of "early pupal stage" is equivalent to the prepupal stage.)

Colony E-101 had done considerable digging to enlarge the chamber under the stone and had piled up a mass of loose dirt about three by eight centimeters along one edge of the stone. The stone was relatively flat, approximately 25 by 40 cm., and a small colony of Crematogaster was under the opposite side separated from the nigrescens by two to three centimeters of dirt. When the stone was lifted, there was some mixing of the two species. The Crematogaster workers quickly attacked six nigrescens and immobilized them by pulling their legs in opposite directions. The army ants were not as successful and did not capture nor noticeably injure any of the Crematogaster.

On 30 June 1955 between 9:30 and 10:30 a.m. Dr. Wallace E. LaBerge and I dug out a large part of the bivouac. Even when the ants were numerous and excited, we could not detect any odor from them. However, when a worker of nigrescens is crushed between one's fingers, there is a strong acid odor similar to formic and glacial acetic acid. More than 20 chloropid flies, Madiza cinerea (Lw.) /det. C. W. Sabrosky7, were apparently attracted to the ants or moist dirt, and these flies both flew above the bivouac and ran on the dirt among the ants.

The mass of workers and the brood of larvae, prepupae and a few pupae together occupied about 250 ml. when alive. At least six tunnels extended downward from the area under the stone, and small groups of ten to 75 pupae were scattered in cracks and small chambers. At a depth of 17 to 20 cm. the queen was found, but there was no large mass of workers nor were the workers more excited near her. However, there appeared to be a slightly higher proportion of larger workers near the queen than elsewhere in the bivouac. The queen was at least partially physogastric with a total length of 14.5 mm. when measured alive. This measurement may not be accurate because the queen was somewhat crushed while we were digging. No strong columns nor clusters of ants could be seen extending below about 20 cm., and no further digging was done. Because only about 2,700 larvae, prepupae and pupae were collected (about half the brood seen), probably a large part of the colony was underground in areas peripheral to the small hole which contained the queen.

When the bivouac was partially dug out, the brood was estimated to be at least three-fourths larvae and prepupae and one-fourth pupae.[1] The larvae were rapidly transforming to pupae, and by the following morning between one half and two thirds of the brood had pupated. By 9:00 p.m. that night over 90% had pupated. Judging from these observations,

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[1] Schneirla (1957a: 126; 1958a: 218) in referring to my observations on colony E-101 stated that a "small sample of mature larvae and a large sample of pupae nearing eclosion" were taken, and the ants "emigrated a few days after maturing worker pupae had been found in the nest." It is not known when that colony emigrated from the site. However, when the ants were <u>first</u> found, the larvae were full-grown and transforming to pupae, and some of these pupae became adults 12 days later in the laboratory. The colony did not emigrate for four days at the beginning of the pupal period, and no subsequent field observations were made to determine when the colony finally did emigrate. Since the queen had been killed and a large part of the brood had been taken, a normal transition from a statary to a nomadic phase would have been unlikely.

the entire period of transformation from larvae to pupae takes about four days and probably at least three fourths of a brood transforms within two days.

In spite of the disturbance of the bivouac, colony E-101 had not left the site by 2 July when an additional layer of dirt and stones five to 15 cm. deep was excavated. Less than 100 pupae were found along with several hundred workers. According to the observations by Schneirla (1958a: 249) in Arizona, nigrescens has a statary phase of 18 days with one brood of pupae, and a second new brood of eggs is laid during that phase. Callow workers of colony E-101 first started emerging on the morning of 10 July which would be the 13th statary day if 28 June is assumed to be the first statary day. However, laboratory temperatures were somewhat above 30°C. during much of this period, and it is quite likely that the length of the pupal period may have been shortened slightly by the temperature. Even though a few callows had emerged, probably several more days would have been required for emergence of at least three fourths of the brood. Since part of the brood appeared to be dying and no workers remained active, the entire brood was preserved. Schneirla (1958a: 233) has reported that a "minority" of the pupal or callow brood was carried on a first nomadic emigration of this species.

A second bivouac (colony E-261) was found on 4 May 1957 a short distance from the bivouac site of colony E-101. This second colony was bivouacked under a stone about 120 by 50 cm. in area with an undetermined number of ants in the soil beneath it. Over 10,000 workers were collected, but no brood nor queen could be found.

Interrelations Among Individuals of Neivamyrmex nigrescens

Queen E-101 was unable to walk, but her legs moved slightly, and her gaster pulsed for more than five hours. Her gaster was split along the left side and a homogeneous white mass (fat body?) and fluids oozed out. Examination with a magnification of 40 to 80x showed no sign of eggs in this mass or at the tip of her abdomen. Workers were attracted to the queen but did not lick any of the fluids oozing from her gaster. The workers primarily licked the knob or ridge on the alinotum and the first and second gaster segments.

The workers of colony E-101 in the laboratory nest gathered most of the larvae, prepupae and pupae scattered in the dirt but ignored many others. The brood was primarily put in three piles on the surface of the soil, and as far as could be determined none was carried into the soil even though the ants made extensive passageways throughout it. The pupae were grasped primarily by their gasters held ventral side up with the mandibles of the adult hooked around the hind tarsi which always were close to the gasters of the pupae. On a number of occasions a worker was seen to turn a pupa completely around end to end and side to side until the adult could grasp the pupa in this preferred position. Much less frequently the workers held the pupae by their heads or gasters with their dorsal sides up.

None of the prepupae nor pupae showed any movement regardless of how much they were handled by the workers or by forceps. When the callow workers started emerging, all the old adult workers which had been collected could scarcely walk or had died. The callows could partially emerge without any assistance, but they walked around encumbered by large pieces of the pupal covering which they could not strip from their bodies. All the callows appeared weak and could hardly walk probably due to the combined effects of hunger and the attached pupal skin.

Cheliomyrmex Mayr

Cheliomyrmex, the fifth genus of Neotropical army ants, includes five extremely rare species placed in the tribe Cheliomyrmicini. The genus ranges from México to Brasil, but too few specimens have been collected to give a clear picture of the range of any species. The first specimen from Panamá is a male of *megalonyx* Wheeler taken at Cerro Campana on 21 October 1959 by Wilford J. Hanson. I determined this male by comparison with the type of *audax* Santschi taken in Ecuador and specimens of *megalonyx* taken at Kartabo, British Guiana, and now in the Santschi collection at Basel. (The single specimen of *audax* which was examined is considered to be the type although there is no type label or collector's name with it.) However, the Panamanian specimen agrees more closely with Borgmeier's (1955) redescription of *audax* than with that for *megalonyx*.

What little is known about the biology of *Cheliomyrmex* is based on the observations by Wheeler (1921: 319-322) on one colony of *megalonyx* found raiding and emigrating at Kartabo. This species of *Cheliomyrmex*, like *Labidus praedator*, makes tunnels on the surface of open ground and has numerous guard workers when it emigrates. Only larval brood was being carried in the emigration column, suggesting that the broods are synchronous. The pupa and queen are still unknown; in fact, no reproductive of any instar has been found in a colony.

III. ARTHROPODS ASSOCIATED WITH ARMY ANTS

Diptera Associated with the Swarm Raids

The family Phoridae has long been known to contain numerous myrmecophiles, many of which have been found only with species of army ants, including _burchelli_ and _praedator_. They are the most common myrmecophiles found _in the raid columns_ of both _burchelli_ and _praedator_, but it has not been possible to determine whether these flies all had left the bivouac earlier, or whether they had found the swarm or a raid column and then followed the columns back toward the bivouac. At the end of a _praedator_ raid, as the ants are retreating down a hole in the ground, I have on a few occasions seen several hundred phorids running among the ants or following after them. Rarely, winged phorids can be seen flying over columns, and it is likely that these are males searching for the normally wingless females. As Phoridae are not ordinarily taken flying about the swarm raids, they will be discussed below in the section Myrmecocoles Found in Bivouacs and Columns.

Among the Diptera that can be collected by sweeping over swarm raids there are numerous families which have no apparent association with the ants, such as the Callobatidae, Chloropidae and Syrphidae. These can be collected in approximately the same numbers by sweeping close to the ground and through the low vegetation in any area of the forest. The family Calliphoridae, on the other hand, appears to be somewhat more abundant over the ant swarms, and the families Sarcophagidae, Muscidae (Anthomyiidae), Conopidae and Tachinidae are clearly much more abundant than in neighboring areas of the forest where the ants are not present (excluding areas with obvious attracting substances such as dead animals or rotting fruit). It is possible that some of these flies are attracted to the noise, odor, or appearance of other flies flying over the ant swarms, rather than to the ants themselves. However, there is one species of Calliphoridae, some Sarcophagidae and some Muscidae which seem to be associated with the ants. At least three species of Muscidae, which are attracted to the swarms, breed in remains of booty deposited by the ants outside their nests. These flies may locate a swarm and then follow the ant columns back to find the bivouac. These muscids are relatively rare at the swarm front but common at the bivouacs. Such forms are discussed in the section Arthropods Found in Refuse Deposits. The most abundant genera, *Stylogaster* (Conopidae) and *Calodexia* and *Androeuryops* (Tachinidae), will be discussed first.

The Behavior of Stylogaster

The genus *Stylogaster* can be readily distinguished from all other Conopidae by the greatly elongated abdomen and ovipositor indicated by the generic name. The genus is so distinctive in this and other respects that Williston (1885: 388) placed it in a separate subfamily where it has remained as the only genus ever since. The most recent or important taxonomic papers on *Stylogaster* are by Aldrich (1930), Lopes (1937), Kröber (1940), Séguy (1946), Camras (1955, 1958), and Lopes and Monteiro (1959). References to other taxonomic literature can be found in these papers.

The genus is found in North and South America, Africa and Asia. About 45 species have been described, but published reports are limited almost entirely to the original descriptions based mostly on few specimens. There are about 15 species known from Africa and Asia, and all are considered distinct from those in the New World. In America the genus ranges from Massachusetts to Bolivia and Argentina. In no locality has this genus been reported as abundant except over swarm raids of Dorylinae. There are scattered records of *Stylogaster* being taken at flowers, and one species, *macrura*, was taken at light (Lopes, 1938: 405). In Africa four people have reported seeing *Stylogaster* hovering over "columns" of *Dorylus* (*Anomma*) [probably *nigricans* or *wilverthi* in all cases] (Brauns in Bequaert, 1922: 282; Bequaert, 1930: 167; Carpenter, 1915: cviii-cix; and Cohic, 1948: 271). (No determination of the insect seen by Carpenter was given, but from its description it presumably was a species of *Stylogaster*.) It is interesting to note that Brauns, Bequaert, and Cohic all reported that the fly was seen hovering over *columns* of the driver ants. It is likely that these observers did not distinguish the basal columns and the swarm front sections of a raid in the sense of Schneirla, but called the entire raid a column. It is important for observers to distinguish between the swarm front, basal columns, and emigration columns since there is some evidence that different flies either prefer or are restricted to these dissimilar aspects of the behavior of the ants. None of the flies observed in Panamá was seen over emigration columns of the army ants. However, emigrations of these ants normally occur only during the night when most Diptera are not active.

In my observations in Panamá, *Stylogaster* was usually seen over the densest areas of the swarm front or in advance of the swarm front by one to two meters. This conopid was occasionally seen over the area of anastomosing columns slightly behind the swarm front but never over the basal columns. *Stylogaster* was present over every maximal swarm observed, but it was not found over a few smaller swarms. Wheeler (1921: 295) and Mann (in Aldrich, 1930: 4) also reported that the species of Stylogaster hovered over the swarm front and apparently not over the columns behind the front. However, Curran (in Aldrich, 1930: 5) stated, "The flies (Stylogaster) were observed to hover over any part of the moving column, and thus differed from the other flies associated with the ants. The Tachinids...were almost invariably found near or in front of the head of the column..."

Stylogaster, by its habitual hovering, could be distinguished from all other flies associated with the swarm raids. At times it would hover for as long as several minutes in one spot and then dart a few centimeters or more than a meter away where it continued to hover. The Stylogaster species are all difficult to see because of their dull coloration, thin bodies, and extremely rapid movement. Consequently, in the dim forest light, specimens often were lost from view as they shifted from one spot to another. On rare occasions a Stylogaster was seen perched on vegetation over the swarms, as was reported also by Lopes (1937: 260). However, it is impossible to state the frequency with which species of Stylogaster rest on vegetation because of the difficulty in finding these motionless flies.

While hovering 30 to 70 cm. above the ground, females of Stylogaster characteristically flipped their abdomens down, or their whole body shifted downward a few centimeters. This movement suggested that the flies were dropping or shooting eggs at the ants below. However, there is no positive evidence that they were ovipositing, and at times it was certain that they were not aiming at any insect, because they continued this behavior over vegetation or bare ground where no insect could be seen. Stylogaster was never seen to dart at the ants alone.

However, on several occasions it was seen to dart after cockroaches, each of which was being pursued by at least five Calodexia (Tachinidae).

Nevertheless, on the basis of the behavior of the flies over the swarm raids three authors concluded that Stylogaster is parasitic on the army ants (Townsend, 1897: 23; Wheeler, 1910: 419; and Mann in Aldrich, 1930: 4). Wheeler (1921: 295) later wrote that he found a "swarm of both sexes of Stylogaster hovering over a spot where there were no Ecitons, although a few workers of Gigantiops destructor and Ectatomma ruidum were running about in the vicinity." He concluded that it is doubtful that the flies are intimately attached to the ants but that they may be attracted by the ants' rank odor. His statement is the only one indicating that Stylogaster is possibly associated with non-doryline ants, and it also is noteworthy for reporting a "swarm" of Stylogaster. I have never seen more than about ten scattered specimens of this conopid per hour, while watching a swarm raid.

Moreover, Mann suggested that Stylogaster attacked the ants in the swarm and not in the raid columns where he thought the more closely massed workers would be more likely to kill the Stylogaster. The behavior of the ants, however, indicates that insects are more likely to be attacked at the swarm front.

A further suggestion that Stylogaster is parasitic on the ants is also open to question. Cohic reported seeing Stylogaster cohici Séguy hovering several times at a height of 10 to 15 cm. and dropping eggs on columns of Dorylus (Anomma) nigricans. He suggested that since these eggs were picked up by the workers and carried into the nests, perhaps Stylogaster parasitizes the nigricans larvae (Séguy, 1946: 99; Cohic, 1948: 271). This would seem unlikely since all other conopids insert their eggs into the bodies of adult hosts on which they are internal parasites. Moreover, the egg of *Stylogaster* is well adapted as a piercing egg rather than an egg which would simply be dropped to be picked up by the host. Unfortunately, Cohic does not state whether he collected any of the eggs. It is possible that he assumed the *Stylogaster* were depositing eggs when he saw them flip their abdomens, and that the eggs he saw picked up by the ants were those of some other fly. Thorpe (1942) has reported seeing *Stomoxys ochrosoma* Speiser on one occasion deposit an egg in front of a worker of *D.* (*Anomma*) *nigricans* which then picked up the egg and carried it toward the nest. It would appear to be impossible to confuse adults of *Stylogaster* with *Stomoxys*, but eggs seen on the ground might be confused. The egg of *Stomoxys* was estimated as two millimeters long, more than twice the size of any known *Stylogaster* egg. The length, thinness, and yellow color of *Stylogaster* eggs make it unlikely that these were the eggs seen by Cohic. Many times in Panamá a species of Muscidae was seen laying eggs near the bivouac of *Eciton burchelli*, and these were seen to be picked up by the workers and carried into the bivouac or to refuse deposits of the ants. However, this fly was not seen to oviposit over the swarm front nor over columns except within a meter of the bivouac. A large series of specimens of this muscid was reared from the material found in the refuse deposits. No reports of similar flies have been found in the literature concerning *Dorylus* (*Anomma*).

Although Curran inferred that the conopids "normally occur singly and associate themselves with the ants as the army travels, their numbers being augmented as the column moves along," he also stated, "There is certainly a close relationship between the flies and the ants."

He concluded that they neither parasitized the ants nor the cockroaches but "... seemed intent only on hovering in patches of sunlight over the army." However, he added that they might oviposit on the ants in the evening, and the eggs would then be carried into the nests where the larvae would feed on the brood (Curran in Aldrich, 1930: 4).

It is unfortunate that Curran (1942: 62-63) emended his note published by Aldrich (1930) by stating that the ants over which he collected the Stylogaster in Panama were not "army ants" but "ant armies" thought to be "entire colonies moving to a new home." He apparently changed this solely because the ants were "much smaller than most Eciton." There are no other non-doryline ants on Barro Colorado Island that Curran could have found "frequently" and in "enormous numbers" moving in swarms across the forest floor. The ants he saw must have been Labidus praedator in which the workers are much smaller than those of Eciton sens. str., and they were undoubtedly raiding rather than emigrating.

My observations support none of the hypotheses of Curran. In watching swarm raids while they were just beginning, I have seen Stylogaster appear in the first few minutes when the swarm front was less than two meters from the bivouac. At other times they were not seen near the bivouac, and on more than a dozen occasions sweeping around the bovouacs yielded no specimens. Sweeping over the area where a swarm raid had completely ceased showed that the flies rapidly dispersed. Approximately a half hour after an area had been teeming with both ants and flies, not a single Stylogaster nor tachinid seemed to be present. This refers primarily to raids of praedator since this species may disappear underground in about 15 minutes, whereas a raid of bur-

chelli ends more gradually. It is possible that *Stylogaster* prefers to hover in the sunlight, but I think one gets this impression because they are easier to see there. Lopes (1937: 260) also records that he saw them flying in the sunlight and resting on vegetation when the sun went behind a cloud. On many occasions I have seen them hover in shade, or move from sun to shade seemingly at random. Nevertheless, it may be true that when they are *not* accompanying the ants, they are more apt to hover in the sun. Curran saw them hovering in sunlight on several occasions where ants were *not* present. I never observed any specimens where ants were not present and took only two specimens by sweeping vegetation where no ants were seen. (We spent more time sweeping where ants were *not* present than we spent sweeping over swarms.) In this connection, Townsend (1897a: 23) reported that in collecting for three months in the State of Vera Cruz, Mexico, he saw *Stylogaster* only on one occasion when he caught 51 specimens. These were all taken over a single swarm raid of *E. burchelli* by sweeping during the last hour or two of daylight. The number of specimens he took indicates a much higher proportion of the flies accompanying the swarm were *Stylogaster* than we found in Panamá. The ratio of tachinids to *Stylogaster*, based on the specimens listed in his papers, is about 1:1, whereas we found about 25:1.

Observations on the behavior of the flies in the evening are more limited because at that time the swarms are usually more poorly developed and thus have fewer flies near them. In addition, it is much more difficult to observe the flies in the dimmer light. On three occasions I observed *Stylogaster* and *Calodexia* near dusk apparently behaving in the same way as earlier in the day. *Stylogaster* was also seen when raids by *burchelli* were just beginning, and only a few scattered sunflecks were reaching the forest floor. On 20 February 1956, when watching one raid start from a bivouac with a brood of worker larvae, I saw the first *Stylogaster* at 7:14 a.m. when the ants had only progressed 0.5 to 1.0 m. from the bovouac. The first *Calodexia* appeared six minutes later.

The number of specimens of *Stylogaster* which we collected on Barro Colorado Island plus one record for *S. stylosa* taken by T. C. Schneirla, are recorded in table . The small number of specimens makes it difficult to draw any conclusions as to whether any species shows a preference for the raid swarms of either species of army ant. One would have expected to find more specimens over *burchelli* considering the greater number of swarms and longer total collecting time over this species. (Approximately 70% of the collecting time was over *burchelli*.) This difference will be discussed more under *Calodexia*. In addition to the species listed in table , the following species have been collected in Panama by C. H. Curran, N. Banks, S. W. Frost, and R. C. Shannon: *apicalis*, *ethiopa*, and *indistincta*. All the Panamanian species were described by Aldrich (1930) except for *ethiopa*, *minuta*, and *stylosa*, which were described by Townsend (1897a). Most specimens of all species from Central and South America have apparently been taken over army ants, but only two authors have given determinations for both the ants and flies. Those known from over *L. praedator* in Brasil according to Lopes (1937) are: *S. australis* Lopes, *ornatipes* Kröber, *rectinervis* Aldrich, *stylata* Fabricius, and *tarsata* Lopes. These species are all different from those found over *praedator* in Panamá. The three species described by Townsend were based on a total of

51 specimens taken over a single swarm of E. burchelli in Mexico. These three species have also been found over burchelli in Panamá (with the possible exception of ethiopa where the species of ant was not given).

Table shows a total of five specimens taken near Eciton hamatum or E. vagans, both of which raid in columns. The two females taken near E. hamatum were observed on 10 March 1955, hovering under a log next to the statary bivouac of colony '55 H-E. Both hovered for a few seconds only 6 to 12 cm. over the ants on the ground next to the bivouac, then shifted to another spot 10 to 20 cm. away so quickly that I could hardly follow them. The flies were not seen to dart at any of the ants, and no eggs were seen to leave the ovipositor (though they might have been missed because of their small size). Stylogaster was never seen near any other bivouac of E. hamatum even though more than 50 nests of this species were watched for brief periods or for several hours. Furthermore, I had pulled many of these bivouacs apart in order to take samples of the brood and myrmecophiles. Following such a disturbance thousands of ants would be milling around the area of the nest and the odor of the colony would be noticeably stronger. There are no published records of Stylogaster near hamatum.

On 9 July 1956, I disturbed a bivouac of E. vagans which had a brood of reproductives approximately at the midpoint of their larval development. Twenty-five minutes were spent thoroughly examining the bivouac and taking the queen and a large sample of the brood and workers. When this was completed, I noticed that about 50 Calodexia and Stylogaster had been attracted to the mass of vagans milling on two or three square meters of ground around the nest. From 10:50 to 11:20 a.m. before I attacked the bivouac, I had watched the raid which had an unusual swarm front of about two square meters quite densely covered with ants. During this time two *Calodexia* and one other fly were seen, but no *Stylogaster*. Following the attack on the bivouac, I swept over the ants milling around the site from 11:45 a.m. to 12:15 p.m., and took three *Stylogaster* and 18 *Calodexia*. Since normally *vagans* is a column raider, the unusual swarm at the head of the raid column was possibly due to the fact that this colony was stimulated to unusual activity by the sexual brood. The fact that the distal end of the raid was also only about ten meters from the bivouac may account in part for the swarm. Otherwise such flies have not been found associated with column raiders but only with the swarm raiders *burchelli* and *praedator*.

These last two cases indicate that *Stylogaster* apparently finds the ants by their odor and can locate at least four species of Dorylinae in this way. This conopid probably is attracted to many colonies but stays only with *praedator* and *burchelli* which maintain swarm raids. This can be considered additional indirect evidence against the hypothesis that *Stylogaster* is parasitic or predaceous on the ants. *E. vagans* and *hamatum* are as big or bigger than *burchelli* and *L. praedator* and should be just as suitable as hosts.

The Life Cycle of Stylogaster

Although no larvae have been described for any species of *Stylogaster*, the eggs of most Neotropical species have been illustrated and described by Lopes (1937) or Lopes and Monteiro (1959). Lopes was the first to show that the eggs have a number of reliable specific characters which alone are sufficient for determining the species. The most outstanding characters of the egg are the shape of the pointed end, the number of recurrent spines (one to four) and the shape of a bladder-like protuberance near that end, and the pattern of reticulations on the surface (figure 75). Because of their value in determining females which are in poor condition, as well as for determining eggs found on possible hosts, it is hoped that future descriptions of Stylogaster females will include descriptions of the eggs.

Stylogaster eggs are most easily removed through the ventral, membranous part of the abdomen while it is still soft shortly after collecting. However, they can also be recovered from dried specimens, though it is often impossible to avoid breaking off the abdomen because of its rather weak attachment to the thorax. The eggs which I examined were partially cleared in a clearing solution modified from that of Nesbitt (1945: 141): 40 g. chloral hydrate, 25 ml. water, 2.5 ml. hydrochloric acid, and 2.5 ml. glycerin. They were then mounted in Hoyer's medium made by the formula given by Baker and Wharton (1952: 10): 50 g. distilled water, 30 g. clear crystals of gum arabic, 200 g. chloral hydrate, and 20 g. glycerin. Clearing in clove oil, cedar wood oil, or xylene followed by mounting in balsam, diaphane, or permount was more time consuming, and the greater permanance of the slides is apparently the only advantage. These latter techniques also require more complete clearing to show the reticulation of the chorion.

All the eggs found in Stylogaster females had completed chorions, and eggs in earlier stages of development were not seen. This is in marked contrast to Calodexia in which larvae and eggs in various stages of development are found in the adult females. The maximum number of eggs in any one female seems to be between 60 and 80. Lopes (1937: 266) reported 60 in S. stylata in Brasil. Neither Lopes nor I found any eggs, either in females or on other insects, showing any sign of larval development except for the one discussed below.

Lopes described an egg of *S. stylata* which he found inserted between the fourth and fifth terga of an undetermined orthopteran. This orthopteran was escaping from a raid swarm of *L. praedator* above which *Stylogaster* had been seen hovering and dashing after cockroaches and other Orthoptera (Lopes, 1937: 259-260, 267-268). Later he reported that when examining the collection of cockroaches at the Instituto de Biologia Vegetal in Rio de Janeiro, Dario Mendes found a *Stylogaster* egg between terga near the end of the abdomen of an adult *Chorisoneura* sp. The species of *Stylogaster* to which this egg belongs is not known (Lopes, 1937: 289-290). Examination of about 50 cockroaches taken on Barro Colorado Island revealed no *Stylogaster* eggs; however, only about ten of these cockroaches were found near army ant raids where *Stylogaster* was present.

After our return from Panamá, the examination of the tachinids associated with the swarm raids revealed eggs of *Stylogaster* on several species of *Calodexia* as well as on *Androeuryops ecitonis* (Townsend). A total of 1802 *Calodexia* and 531 *Androeuryops* were examined and 17 *Stylogaster* eggs were found, one per fly. Thus, less than 0.8% of the tachinids had *Stylogaster* eggs on them. A summary of these records is given in table . Of the 17 eggs found on tachinids, seven are *S. currani* and five are *S. minuta*. These are two of the most common species of *Stylogaster* found (cf. table). However, *S. banksi*, one of the most common adults, was represented by only a single egg. The significance of these data is subject to considerable doubt. At least most of these tachinids are large enough to serve as hosts but *Calodexia fumosa*, *C. panamensis*, and *A. ecitonis* would appear to be too small. However, the *Stylogaster* eggs on these three tachinids all belong to *minuta* which is the smallest of the species involved. This correlation in size may indicate that the small species of the tachinids and *Stylogaster* parasitize the same host (which may be smaller than the hosts of the larger flies), and that the *Stylogaster* lays some eggs on tachinids by mistake.

It is also noteworthy that of the 17 eggs, 7 were found on *Calodexia agilis* and 3 on *C. dives*. The incidence of eggs on these two tachinids is clearly much higher than would be expected if the eggs were laid at random on the flies. (The number of specimens for each species of tachinid is given in table .) Here again, the distribution of the eggs may be explained if the tachinids parasitize the same host as the *Stylogaster*.

The position of some of the *Stylogaster* eggs indicates that they may have been inserted accidentally into the tachinids. For example, several were found on eyes or wings. Nevertheless, in ten of the 17 cases, the eggs were found in the intersegmental membranes between abdominal terga. This is the same relative position as the two eggs reported by Lopes on Orthoptera. All the eggs were firmly implanted in the tachinids. Those in the eyes were inserted below the level of the recurrent spines on the sides of the eggs, the ones in intersegmental abdominal membranes were usually implanted for one-third to one-half their lengths. It would appear likely that if the eggs were accurately placed in a membranous area, they might penetrate completely inside these insects. Judging from the darker areas of cuticle around the sites where the eggs had penetrated the host, most of these eggs had probably been in the tachinids for several days.

Among the specimens of Calodexia examined there were about 20 which had abnormal abdomens. Included among these were flies with puncture wounds in the sides of terga, flies with asymmetrical bulges between terga, and flies with two terga fused together. These abnormal abdomens were all dissected, but no Stylogaster larvae nor internal parasites of any kind could be found in any of them.

Of the 17 eggs found on tachinids, only one egg showed development, but this was noticed only after the egg had been cleared and mounted in Hoyer's medium. This egg contained a first instar larva emerging from the blunt end of the egg, which thus must be considered anterior (see figures 75 to 77). Although Lopes (1937) has considered the pointed end to be anterior, the eggs are arranged in the abdomens of the females with the pointed ends directed posteriorly. This would not only be the logical orientation for oviposition, considering the shape of the eggs, but also would indicate that the blunt end is morphologically anterior, since eggs are normally arranged in oviducts in this position.

Near the pointed posterior end of the egg, a bladder is everted only after the egg is deposited, and perhaps contact with moisture or the physical stimulus of being forced into the host is necessary before the bladder will evert. Eggs removed from the abdomen of a Stylogaster will evert this structure after they are cleared if pressure is applied to the side of the egg. One function of this bladder must be to help hold the egg in the host. It also may be used to absorb fluid or other materials from the host necessary for further development of the embryo. Lopes (1937: 268) concluded that the larva must enter the host through this structure, but the discovery of the egg with a larva emerging from the opposite blunt end makes this hypothesis unlikely. Eggs removed from a female show no indication of a weaker area at the blunt end. However, after they have been softened and cleared, pressure on the side of the egg will cause the blunt tip to bulge out revealing a weaker region at that end. There is no distinct operculum, and the larva apparently ruptures the end of the egg with its oral hooks (possibly after dissolving part of the chorion). The end of the egg illustrated in figure 75 shows a thin, frayed edge around the opening through which the larva is protruding.

The buccal armature of the first instar larva, illustrated in figure 77, differs considerably from the few conopid larvae which have been described by de Meijere (1904), as well as from most higher dipterous larvae. These other conopid larvae, both in the first instar and in later instars, have one, two, or three large oral hooks which may or may not have small teeth on them. However, in the Stylogaster larva the oral hooks appear to have fused into a single hook with many large, hook-like, teeth of approximately equal size. The pharyngeal sclerites (terminology of Roback, 1951) are separate posteriorly but fuse together before they articulate with the oral hook.

Three possible second instar larvae of Stylogaster were found under the following conditions. A cockroach, Eublaberus posticus (Erickson), taken in the forest, but not near a swarm raid of army ants, was used for an experimental introduction of about 12 larvae from a female Calodexia venteris Curran, on 30 July 1956. Five last instar larvae of C. venteris were found outside the still-living host on 5 August, but on the next day the cockroach died. Larvae were still seen within the cockroach, and therefore, it was not preserved until we were about to leave Panama on 18 August. Subsequent dissection revealed 16 additional larvae, and three of these are thought to be Stylogaster (2236). (Numbers in parentheses are field numbers for specimens.) Each of these three larvae has a large median, ventral oral hook and two lateral oral hooks. Each lateral hook has about seven elongate, curved teeth which look like a reasonable development from the cluster of more blunt teeth illustrated in figure 77. These three larvae do not look like any known larvae of Calodexia. Each "Stylogaster" larva has a pair of rather simple posterior spiracles without large spiracular plates. This arrangement of spiracles would be expected in a second instar conopid larva, but other parasitic larvae also have similar spiracles. Third instar conopid larvae probably would have larger, more sclerotized spiracular plates. In addition, both the first instar and the "second instar" larvae have a pair of similar "antennae" on the pseudocephalon. No Stylogaster eggs were seen on the cockroach when it was examined prior to the introduction of the Calodexia larvae nor when it was later dissected. Two attempts to rear Stylogaster by introducing eggs into a cockroach, Eurycotis sp. (2246), and a cricket, Ponca venosa Hobard (2245), were unsuccessful.

In addition to evidence given above on possible hosts of Stylogaster, there is the incorrect statement by Brauer and Bergenstamm (1893: 84) that Bates (1863) records Stylogaster pursuing termites. Bates (1863, v. 2: 366) in discussing Stylogaster makes no mention of termites, and it has been impossible to find any first hand observation to support termites as a host. Bequaert (1922: 281) calls attention to this error and cites three repetitions of this mistake including the frequently cited classic paper by de Meijere (1904). Bequaert's paper has not had appreciable effect on subsequent reviews. Additional repetitions of this erroneous host record are found in works of Röder (1892: 287), Aldrich (1930: 4), Lopes (1937: 259), and Séguy (1949: 99).

The hypothesis of Townsend (1897a: 23) and other authors that the army ants are the hosts of *Stylogaster* is not supported by the behavior of the flies discussed above. In addition, examination of about 150,000 workers of *burchelli*, about an equal number of larvae and cocoons of *burchelli*, and about 25,000 workers of *praedator*, has revealed no *Stylogaster* eggs nor larvae which might be *Stylogaster*. Eggs may have been overlooked in examining these ants, but they must be very scarce if present at all. The worker ants are probably too small for the development of *Stylogaster* and development on queens or males would be impossible, since only a single queen is usually present in a doryline colony and males are only present for a brief period during the year.

No one has even suggested a host for any *Stylogaster* species which has not been found associated with ants. It is significant that the range of *Stylogaster* extends beyond the range of *Eciton* *burchelli* and *Labidus* *praedator*. This is seen most clearly in the United States where the genus can be found as far north as Massachusetts, far outside the range of any doryline ant.

In summary, it appears that the most likely hosts for *Stylogaster* are cockroaches and possibly other Orthoptera. Some species may be parasitic on Tachinidae, or the eggs found on them may be solely accidental. A seemingly less likely hypothesis would be that these eggs hatch and the larvae get on their true hosts when the tachinids parasitize the same host. The one case cited above of both "*Stylogaster*" and tachinid larvae in the same host would indicate that they are not incompatible, though the "*Stylogaster*" did not develop to maturity. The failure of all the larvae to develop in this instance is quite likely due to the large number (21 or more) of larvae in the relatively small host.

The *Stylogaster* species which are found over army ant swarms probably are not absolutely dependent upon the doryline ants in any way. However, it appears that their association with the ants gives them a major advantage in finding their hosts. Without the ants to flush out the Orthoptera, *Stylogaster* would apparently have to be present at the moment when a potential host runs from cover. Some species of *Stylogaster* might be unable to find their hosts because of the secretive nature or nocturnal habits of cockroaches. However, the *Stylogaster* species which are not associated with ants, such as the species found in the United States, may be parasitic on Tachinidae or Orthoptera which are more easily found.

Androeuryops

Townsend (1897b) described the Tachinid, *Hyalomyia ecitonis*, from a series of flies collected by sweeping over a swarm raid of *Eciton foreli* (=*burchelli*) in southern Mexico. Beneway (1960) has examined part of the type series and has based a new genus, *Androeuryops*, on these specimens. *Androeuryops ecitonis* was also found in large numbers over swarm raids of both *burchelli* and *praedator* in Panamá (see table). As in some of the species of *Calodexia* discussed below, the proportion of *A. ecitonis* found over *burchelli* was much higher than would be predicted on the basis of the time spent collecting over the two ant species. Of a total of 531 specimens of this species, only two were collected by sweeping where there were no ants. In marked contrast to

Calodexia in which almost all specimens which were collected over swarms are females, 345 specimens, or almost two-thirds of the Androeuryops taken, were males.

Although the populations of Stylogaster and Calodexia remained rather constant from February to August, there was a great change in that of Androeuryops. From February through about the first half of May, Androeuryops was very abundant, and more than 20 specimens could be collected in 15 minutes over an average sized swarm of burchelli. The maximum abundance was observed on 16 February 1956, when in one hour 216 specimens were taken over a single raid. From 25 May to 18 August the maximum number taken in a 15 minute period was nine specimens. Even when over 100 Calodexia were taken, only an occasional Androeuryops was found. Therefore, for unknown reasons, Androeuryops is abundant in the dry season and early rainy season and then rapidly decreases in abundance. This seasonal fluctuation was so marked that it probably was not unique to 1956. A complete list of the records for Androeuryops ecitonis is given below in the "List of Field Numbers with Collecting Data for Flies."

The adults were not seen to hover like Stylogaster, and on only two occasions were they seen to fly after cockroaches. In both cases the cockroaches were also being pursued by Calodexia. The large number of specimens found from February to May and the constancy of their presence over the swarms, but not near the bivouac, indicate that they are definitely associated with the army ants. Probably they are parasitic on some arthropod flushed out by the ants. The female lays eggs and probably inserts them within the host judging from the large, pointed, and heavily sclerotized ovipositor. Both the egg and ovipositor have been described by Beneway (1960).

The Behavior of Calodexia

The tachinid genus *Calodexia* includes 13 species which have been taken on Barro Colorado Island over swarm raids of *Labidus praedator* and/or *Eciton burchelli*. Whereas *Stylogaster* females appear to outnumber the males slightly, 1783 females but only five males of *Calodexia* were taken over swarms. Curran (1934a: 1-2) also reported that the males "are seldom, if ever, found associated with ants" and "are remarkably rare considering the abundance of females." In his extensive collecting of Diptera on Barro Colorado Island, Curran found males resting on vegetation not near ants and collected 20 specimens, compared with about 150 females taken over ant swarms. I found only one male on vegetation where no ants were seen. Two series of *Calodexia* which were reared included a total of six males and five females, suggesting that the unusual sex ratio near ants is based mainly on a difference in the behavior or survival of the adults.

Like *Stylogaster*, *Calodexia* appears near the bivouac when a swarm raid is starting and stays with the swarm front as it advances. However, *Calodexia* never hovers for more than an instant and normally rests on the low vegetation in the middle of the swarm of ants. *Calodexia* is not as easily frightened away as *Stylogaster* and sweeping over a raid swarm intermittently for an hour does not seem to diminish the number of tachinids. It is also possible to collect them with an aspirator when they are resting near the swarm front.

As the swarm advances farther from the bivouac, the width of the swarm front also normally increases to a maximum of 10 to 15 meters.

At the same time the *Calodexia* and *Androeuryops* become more numerous. This is shown by the collection series (1170-1172 and 1411-1415) where sweeping was done in three and five successive timed intervals over two swarms and the flies recorded separately for each period. On one day during the first 30 minutes of sweeping (9:45 to 10:45 a.m.) 19 *Calodexia* and 36 *Androeuryops* were taken. During the two following 15-minute periods the numbers of *Calodexia* increased to 22 and 34 and *Androeuryops* increased to 53 and 127. Over the other colony flies were taken in five 15-minute periods starting at 10:00 a.m. The *Calodexia* totals are: 16, 15, 31, 49, and 13. The *Androeuryops* totals are: 7, 14, 37, 32, and 24. The decrease in the number of flies during the last period from 11:00 to 11:15 a.m. is correlated with a decrease in raid intensity as the ants entered the siesta period.

On one occasion a winged cockroach was flushed out by a *burchelli* swarm, and the cockroach was seen to jerk away as three *Calodexia* darted at it as it ran ten centimeters up a small plant. A few seconds later while one fly hovered for an instant over the abdomen of the cockroach, the other two sat on the leaf only three centimeters from the cockroach. The ants then captured the cockroach. Although the *Calodexia* hovered over cockroaches or crickets, they darted at them only when the orthopterans were running or flying. Several *Calodexia* would rest near motionless Orthoptera without making any attempt to attack them until they started to flee. With winged cockroaches the attack in flight may be necessary in order to deposit the larvae directly on the abdomen or under the edges of the terga. However, the flies also waited for wingless cockroaches to move before they would attack. It seems likely that they are able to see most of these cockroaches since the flies hovered directly over them. From the standpoint of survival of Calodexia larvae, it would naturally be important to get them on healthy, not injured or dead, hosts. Although the Calodexia flew after cockroaches and crickets they showed little interest in the numerous spiders which ran from the swarm fronts. At times they flew about 30 cm. after a spider but then turned away and rested on a leaf. None of the flies showed any attraction toward amphipods, isopods, phalangids, scorpions, millipeds, centipedes, reduviids, coreiids, pentatomids, cicadas, nor scarabaeids. These are among the more common other arthropods flushed out by the ants, and the number of observations on each of them at the swarm front varies from three to 30 or more.

The species of Calodexia all behave similarly with respect to their positions around the ant swarm. They are seldom in the fan area but always can be found throughout the area where the ant swarm is most dense as well as in advance of the front by about two meters. If in the fan area, they were usually in small groups around or hovering over Orthoptera being attacked by the ants. The only times that the different species appeared to show any species-specific behavior was when an occasional cockroach or cricket ran from the ant swarm. On a few occasions when it was possible to get close enough, it was noticed that flies of only one size were pursuing an orthopteran. None of the species of Calodexia are distinctive enough to make specific recognition possible in the field. However, since some are more then twice as large as others, on a few occasions it was possible to note that as many as three species were attracted to a single cockroach.

The species of Calodexia all rest close to the ground and seem to be found on vegetation more than 50 cm. from the ground only when lower perches are not available. The flies will rest on the ground but apparently prefer slightly elevated perches. They frequently rest on fallen leaves, especially where the edges and tips are curled away from the ground. Ants are continually running up on their perches, and the flies constantly shift, usually avoiding contact with the raiding ants. At times the ants touch a Calodexia with their antennae or legs, but no adult fly was ever seen captured, nor were they ever found among thousands of pieces of booty examined. When the flies shift to a new perch to keep up with the swarm or to avoid the ants, they seem to land on any open surface. Then they usually shift position in order to face downward, but they did not seem to show any preference as to whether they faced toward or away from the direction in which the swarm front was moving. At times Calodexia is so abundant that there are about ten flies in an area 30 cm. square. In such cases, whenever one fly shifts position a few centimeters, or another one lands nearby, many of the flies in the immediate vicinity fly at least ten centimeters to a new spot.

On every occasion when I have observed the start or end of a burchelli or praedator swarm raid, the suddenness with which these flies appear or disappear has been impressive. Sweeping throughout an area with a radius of ten meters from a burchelli bivouac revealed no Calodexia, or at most about ten specimens. Ten to twenty minutes later, when a small swarm raid had advanced only a few square meters, more than 50 Calodexia could be found near the swarm front. Apparently they have a good sense of smell and probably spend much time flying through the forest whenever they are not accompanying a swarm. It seems strange that they were not found more frequently near the bivouac itself.

Although the number of flies increases as the swarm front develops during the morning, this increase in numbers is dependent more on the size and intensity of the raid rather than on its duration. The number of flies decreases during the siesta period even though at that time the raid has been in progress for several hours and the ants are spread out over the maximum area. The changes in the number of flies may be dependant upon changes in a "raiding odor" or some stimulating chemical produced by the ants which not only excites the ants, but may also attract the flies. A bivouac of burchelli has a much stronger odor than a raid to the human sense of smell, but this may not be true for the flies.

When rain interrupts a swarm raid many of the ants go under leaves, and others return to the bivouac. Calodexia also will go under leaves, but a surprising number of them stay on the upper exposed surfaces, and as they get splashed by the rain drops, they wipe the droplets off their bodies with their legs.

When sweeping for flies over the ants, even though no attempt was made to sort the specimens as soon as they were collected, it was immediately evident that several swarms of L. praedator had a much higher proportion of the larger species of Calodexia than did burchelli swarms. Later, when all the specimens had been sorted, distinct differences among the species of Calodexia associated with the two species of ants were found, as summarized in table . It was estimated that approximately 770 minutes were spent sweeping over swarm raids of burchelli and 325 minutes over praedator (based on the total time of intermittent sweeping and transferring specimens to killing bottles). Almost all collections were made between 10:00 a.m. and noon when the swarms are largest and the flies most active. A list of the dates and times when these collections were made is given at the end of this paper. These data were analysed by the G-test (Woolf, 1957; Kullback, 1959) to determine if the numbers of flies of each species collected over the two species of ants differed significantly from the proportion expected on the basis of the time spent sweeping over these two species (770:325). The values for G were compared with the Chi-square distribution which closely approximates that for G. It is interesting that these comparisons all show either no significant difference from what might be expected based on the total collecting times, or else they are highly significant, with no borderline cases. It is clear that six of the 12 species tested show a preference for one or the other ant species, and in two cases, dives and panamensis this is especially marked.

The biological significance of these results is doubtful. It is possible that some species of Calodexia are attracted to one species of ant more than to the other on the basis of the odor differences of the ants with no survival advantages for the fly. However, for certain species of Calodexia, there may be an advantage attributable to the different raiding behavior of the ants. The more subterranean Labidus praedator clearly raids to a larger degree under leaves and other objects which are close to the ground. Because of this difference in raiding, it is probable that praedator drives out some species of arthropods which are not often disturbed by burchelli. The workers of praedator are smaller than those of burchelli, and the former appear to capture more smaller arthropods while perhaps missing more of the larger orthopterans. In addition, burchelli raids more frequently and much higher up trees, going near the tops of the tallest trees more than

30 meters from the ground. It is not known whether any of the flies follow the swarm raids in these trees, but this arboreal raiding must drive out many arthropods not found on the forest floor. Other than the gross behavior of the ants, there is no evidence for a difference in the proportions of potential hosts driven out, since no quantitative nor qualitative study of the arthropods either driven out or eaten by the ants has been made. Knowledge of the hosts may eventually support the observed differences in the proportions of the different *Calodexia* species associated with the two species of army ants. However, at this time no reliable conclusion can be reached because far too few hosts are known.

In addition to *Calodexia* associated with *burchelli* and *praedator*, two specimens were found near the unusual swarm raid of *Eciton vagans* (discussed earlier, under *Stylogaster*). After the bivouac of this colony was located and, the queen, a large sample of the workers, and part of the sexual brood were taken, it was discovered that *Calodexia* had been attracted to the ants milling around the bivouac site. About 50 flies were in the area and 18 were taken. In contrast to this experience with a disturbed bivouac of *vagans*, no *Calodexia* could be found near the ants milling around more than 20 nests of *E. hamatum* which had been similarly disturbed. As with all other species of *Eciton*, the odor from a bivouac of *E. hamatum* becomes much stronger when the ants are disturbed.

The Life Cycle of Calodexia

Although *Calodexia* is much more numerous around the swarm front than *Stylogaster*, there are fewer records of its presence and less speculation about its biology. This is probably due to the unusual morphology of *Stylogaster* and the fact that the Tachinidae are poorly known taxonomically. *Calodexia* is not conspicuously different from hundreds of other genera of higher Diptera, and very little work has been done on the taxonomy of the genus even though it is widely distributed from Mexico to Brasil (and probably Argentina). The most extensive previous collection was made by Curran, who has also described most of the species of *Calodexia*. He gave only brief comments on their association with army ants and decided that the flies parasitized cockroaches since they flew after them (Curran, 1934a: 1-2). Curran did not know whether *Calodexia* deposited eggs or larvae and did not identify any of the ants or cockroaches involved. The only positive information on their life cycle was given by Lopes (1937: 260) who reared "*Calodexia ?venteris*" from one specimen of *Periplaneta americana*, apparently taken as it was escaping from a swarm raid of *Labidus praedator*.

All females of *Calodexia* which were examined had more than 25 larvae in their oviducts, and some had over 200 arranged in dense, continuous spirals, showing progressive development from small eggs to actively squirming larvae. It is very easy to slit the membrane between the first and second abdominal segments and remove the posterior segments from either a dried or fresh specimen. Dried abdomens then can be softened in hot water or Nesbitt's clearing solution and the oviducts and larvae removed. Larvae from dried specimens are readily expanded and cleared in Nesbitt's solution and can be mounted directly on slides in Hoyer's medium. (See the section on "The Life Cycle of *Stylogaster*" for formulas of these solutions.) First instar larvae of eight species were examined; these all showed specific characters.

The first instar larvae have an indistinct pseudocephalon which lacks spines and shows no clear separation from the first thoracic segment. (The terminology for the larvae used here follows that of Roback /1951/.) The three thoracic segments have very fine spinules in segmental bands and some species have ventral patches of strong spines on the meso- and metathoracic segments. All first instar larvae examined have strong bands of abdominal spines. These bands are composed of about five rows of spines of varying lengths and shapes, arranged so that the spines are contiguous for most of the width of the larva. The arrangement and shape of these spines are useful for separating species. There are hooks at the posterior end of the body near the simple posterior spiracles, and these hooks probably are used to hold on to part of the host's tracheal system. The buccal armature is thin and long with broad or long, thin, sharp hooks. These larvae appear well-adapted for piercing a host and for moving on most surfaces. Females dropped larvae when they were etherized, killed in cyanide bottles, or if their abdomens were squeezed. These larvae were very active when they came out of the female. Probably they are dropped on the surface of the host and then burrow into it, since the larvipositor of the female shows no piercing adaptations. Although all instars have excellent specific characters among the few species where more than the first instar is known, there do not seem to be any specific characters which are stable throughout the larval period. Therefore, it is impossible to identify later instars by comparison with the larvae removed from adult flies.

The second instars lose the prominent bands of spines but retain bands of spinules or roughened areas. The oral hooks become much broader and very different in shape, prothoracic spiracles develop, and there is a prominent papilla (antenna?) at each anterolateral angle of the pseudocephalon. The third instar larva has a pair of large posterior spiracular plates with peritremes which are almost closed. A button and three elongate, almost straight, spiracular slits are found on each plate. The oral hooks are shorter and broader than in the second instar and there are two small holes in the central area of the basal part of each hook. The ventral edges of the hooks may have a series of fine teeth.

Only one series of Calodexia was reared to adults from a determined host parasitized in the forest under natural conditions. This series of eight C. interrupta was reared from a gryllid, Ponca venosa Hebard (2260-X), which was taken as it was running from a swarm raid of burchelli. Three to five adults of Calodexia were seen to fly closely after the cricket as it ran about a meter in advance of the ants. This cricket was taken on 7 August 1956, and on 11 August nine puparia were found in the rearing vial. Four males emerged on 21 August and four females on 22 August. No fly emerged from the ninth puparium, and no additional larvae could be found in the cricket. Thus, the larval stage was very short, with a duration of about four days; and the pupal stage lasted 10 to 11 days. No larvae were found in four additional specimens of Ponca venosa (2231, 2157) which were dissected 4, 6, 16, and 28 days after groups of Calodexia were seen flying after them in front of raid swarms.

In addition to this one case where the species of both host and parasite are known, there are several less complete cases. One Calodexia pupa was reared from a cockroach (2259) taken on 1 August as it was running while pursued by L. praedator and Calodexia. The cockroach died on 5 August, and the single puparium was found on 6 August, but no adult emerged. The oral hooks from this puparium are very similar to those from a known C. venteris puparium, but positive identification cannot be made until other puparia are available.

A gryllid, Eneoptera sp. (2205), taken as it was running away from a swarm raid of Labidus praedator on 27 July, was dissected on the same day. Three first instar Calodexia larvae near agilis or interrupta were found inside near the dorsum of the first abdominal segment. These larvae were not firmly imbedded nor attached to any tissue, but they may have shifted in position after the cricket was killed. A second Eneoptera sp. (2184) taken under similar conditions was dissected 60 hours after the time of suspected larviposition. Three small second instar larvae and nine early third instars, perhaps of the same species, were found in it. In a third specimen of Eneoptera (2231) taken in similar circumstances no larvae could be found.

Two cockroaches, Epilampra azteca Saussure (2069-A, 2069-B), were taken escaping from a praedator swarm on 5 July. One was dissected that day and no larvae were found in it. The second specimen was dissected 24 hours after the time of suspected larviposition, and nine larvae were found in it. All these appear to be second instar Calodexia larvae. These larvae were found close to the abdominal body wall of the cockroach except for one or two which were either close to the gut or were pulled away from the body wall when the cockroach was dissected. A subsequent attempt to introduce Calodexia larvae into a specimen of Epilampra azteca (2295) was unsuccessful and when it was dissected after eight days, no larvae could be found.

A cockroach nymph (2069-C) which could not be identified to genus was taken at the same time as the above mentioned Epilampra. When it was running from the ants, it was clearly seen to be pursued by several females of one of the largest species of Calodexia and by no other flies. A puparium was found on 15 August in the rearing vial with this cockroach, but the larva probably came out of the cockroach several days earlier. No adult emerged from this puparium. In December 1959 the puparium was dissected and an advanced, but light-colored, female pupa of Calodexia dives was found in it. In spite of the incomplete development this specimen could be determined since it is the only Calodexia which lacks presutural acrosticals and has one pair of postsutural acrosticals. Although other species of Calodexia were flying nearby, it is noteworthy that only large Calodexia were seen to pursue these last three cockroaches. However, the nymph in which the dives developed was a small host, only about 15 mm. long. On one occasion a single C. dives was taken as it and at least two other smaller species hovered over a cricket (?Ponca venosa) being attacked by the ants.

About 12 larvae from Calodexia venteris were introduced into each of two specimens of Eublaberus posticus (Erickson) (2235, 2236) on 30 July 1956. On 5 August four puparia and one mature larva were found outside of the second cockroach, and two males and one female C. venteris emerged from these puparia on 18 August. Although the cockroach appeared weak, it remained alive until 6 August. It was not preserved in alcohol until 18 August, however, since additional larvae were still seen inside it. When the cockroach was dissected, four first or second instar larvae were found which were probably laid on the cockroach after it died. Nine second instar larvae, which might be Calodexia, and the three larger second instar larvae, which were discussed above as possible *Stylogaster*, were also found.

In hopes of rearing specimens of males, which are almost impossible to find near the ant swarms, *Calodexia* larvae were introduced into additional insects which were readily available at the laboratory. The following insects were tried: prepupae and pupae of *Polistes* and a sphecid muddauber, tettigoniids (*Chloroscirtus discocercus* Rehn, *Euceraia* sp., *Microcentrum stylatum* Hebard, *M. philammon* Rehn, *Microcentrum* sp., and *Phylloptera dimidiata* Brunner), gryllids (undetermined nymphs), and cockroaches (*Eurycotis* sp., *Periplaneta brunnea* [Burm.], and undetermined nymphs). No larvae completed development in any of these "hosts", although in a few cases they were seen moving under the body wall for at least a day following the insertion of the larvae. Several first instars at least doubled in size, and two *C. fumosa* larvae (2242-C) developed to second instars in a tettigoniid which died a few hours after they were inserted.

In summary, the known fragments concerning the behavior and biology of *Calodexia* indicate that the different species are all larviparous and internal parasites of Blattoidea and Gryllidae. The larval period is only four or five days and the pupal stage lasts ten or 11 days. These were reared under fluctuating laboratory conditions at around 28° C which is slightly warmer than forest floor temperatures. Even allowing for the possibility that some first instar larvae were overlooked in dissecting the hosts, it is clear that of the cockroaches and crickets which escape the ants, 50% to 90% are subsequently parasitized by the flies accompanying the ants. In most cases this parasitism is fatal to the host.

Observations on the Taxonomy of Calodexia

All 23 known species of Calodexia are included below in a table of diagnostic characters and a key. Additional records and clarifications of the original descriptions are also given for all species found on Barro Colorado Island. Nine species in the genus have not been examined by the author, and the brief treatment of them is abstracted from the published descriptions. About 170 specimens, representing thirteen species, were previously known from Barro Colorado Island. Since most of these species were based on few individuals, examination of 1802 additional specimens from this locality has revealed a few errors and more variation than reported in the original descriptions. Possible geographical variation is not involved here because all the specimens are from the type locality except for the specimens of similis and fumosa.

In the generic and specific diagnoses given below, all characters which are not mentioned are considered to agree with the original descriptions. Only additions or major modifications of the descriptions are included. Information on specific characters which can be easily presented in table   is not repeated in the comments for each species unless some clarification seems desirable.

Throughout the present treatment the terms used by Curran (1934a, 1934b) have been used, but in some cases modifications of these terms have been made in an attempt to be more precise. The method of describing the arrangement of bristles follows that used by many dipterists, e. g., acrosticals 1-3 means that there is one pair of presutural and three pairs of postsutural acrostical bristles. The term frontals is used for the row of bristles along the inner edge of the parafrontals and includes both the proclinate and reclinate orbital bristles. The width of the eye is measured perpendicularly to the median margin of the eye when the head is observed perpendicularly to the anterior surface. Abdominal terga are numbered as in Curran, i. e. the "first tergum" is the first obvious segment, but morphologically, it is the second tergum. Other terms are explained here with reference to table , and the abbreviations used in that table are given in parentheses. A question mark (?) indicates that the state of a character cannot be determined with certainty from the published description. Where several states are included for the same character, the most common state is underlined; e. g., number of bristles <u>2</u>-3. This indicates most specimens have two bristles, but an occasional fly or possibly as many as ten percent of the specimens have three bristles. Where fractions are used, e. g., 1/2 (abbreviated as 1), 2/3 (2), the abbreviation 1-2 means from 1/2 to 2/3. For all thoracic and abdominal characters using patterns of pollen or vittae, the specimens should be viewed with the light striking the specimen at a slightly posterior angle. Small bristles have been included in the counts of bristles when they are only slightly larger than neighboring hairs and in the "correct positions." When looking perpendicularly at a section of body wall using a microscope with a bright light and 40x magnification, "white" hairs usually cannot be seen although they can be seen when the specimen is turned more obliquely to the line of sight. "Black" hairs can be seen in perpendicular view as well as in oblique view and are usually shorter and coarser than white hairs. "Black" hairs in some lights have a brownish or reddish sheen.

Throughout this paper the following colors are referred to only by the primary color: orange, usually a dull, pale, slightly brownish-orange (o); yellow, a dull, pale straw color or slightly brownish yellow (y); gold (g); brown (br); black, due to pollen often appears brownish in some lights (b); bluish (bl); white to pale gray-white (w). Combinations of these symbols are also used; e. g., (obr) = orange-brown; (o-br) = orange to brown (where color varies from orange to brown in a single specimen or species). All observations were made with a stereoscopic microscope using 40X magnification and a fairly bright light (Spencer microscope light). Under lower magnification and dimmer light the colors look darker and closer to the colors as given in Curran (1934a).

Notes applicable only to an individual character are given below and are numbered to correspond to the numbers in the left hand column of table .

1. Color of occipital pollen: mostly white to yellowish on posterior aspect of head, but dorsal and median black bands of pollen may be present (w); mostly black, but lateral edges may be whitish (b). Specimens should be examined laterally to see maximum amount of white pollen.
2. Downward extent of row of black bristles along outer edge of occiput measured as fraction of length of eye: fractions 1/2, 2/3, 3/4, and 4/4 (extending completely under eye) are abbreviated as 1, 2, 3, and 4. Head is observed laterally to determine length of eye and extent of occipital bristles.
3. Width of palp: nearly equal throughout its length or enlarged apically to about twice the width of basal half (e); greatly

enlarged near apex to three or four times width of basal half (en).

7. Anterior outer dark vittae of mesothorax: do not extend anteriorly to reach the position of median sublaterals (ne); extend to level of median sublaterals (es); extend anteriorly beyond position of median sublaterals (ea). Where outer dark vittae are greatly narrowed but continued as fine lines to anterior surface of thorax, only broad main vittae are considered. Where there is a darker stripe in the middle of an area lacking white pollen, the entire dark area is considered to be the vitta, not only the darker stripe.

8. Median postsutural dark vittae of mesothorax: united for approximately their entire lengths to form a single broad vitta, but median section of this vitta may be more grey or have a few light pollen spots (u); separated directly behind suture by light pollen but joined posteriorly for about one-half their lengths (sbs); separated for entire lengths behind suture (sel).

9. Light colored postsutural mesothoracic vittae which separate outer dark vittae from median dark vittae: absent, so that all postsutural dark vittae are united for at least half their lengths, usually appearing as wide solid black fascia across thorax behind suture (a); narrow, at widest point about half width of an outer dark vitta (n); about equal in width to an outer black vitta (e).

11. Marginal scutellar bristles include lateral bristles and large pair on posterior lateral angles of scutellum but not apical marginals. (Townsend /1912: 309/ includes posterior lateral marginals with

apicals.)

14. Infrasquamal cilia are sometimes reduced or absent.

20. Posterior femora when seen ventrally: only proximal one-third to three-fourths orange (po); or color of entire ventral surface except distal extremity (o, br, etc.). Specimens should be turned to view posterior femora from several angles to see maximum amount of light color in ventral view.

21. Ventral yellow cilia are arranged in more distinct rows than majority of hairs on ventral surface of femur, and longest cilia are at least as long as thickness of tibia. Few scattered hairs on inner or outer central margins not considered to be rows unless they extend along at least half length of femur.

22. Color of shining dorsal abdominal pollen (ignoring duller gray-white pollen). Specimens examined with light striking dorsal surface approximately perpendicularly to give brightest and most highly colored reflection from pollen.

23. Color of dorsum of first tergum (ignoring pollen): orange, may have a weak middorsal dark stripe (o); orange with strong middorsal dark stripe about as wide as distance between marginals (os); entirely brown (br); or black, usually with brown pollen (b).

24. Whitish pollen on dorsum of first abdominal tergum: abundant and dense at any point in dorsal view (dwp); absent or sparse (a).

25. Light pollen of ventral areas of both first and second abdominal terga: equally white and dense (e); absent or much less white and less dense on first compared with second tergum (a); absent or weak on venters of both terga (aa).

26. Pale pollen on second abdominal tergum: not interrupted by median longitudinal stripe (ni); interrupted for almost entire length of tergum by narrow dark or pollenless median stripe less than half as wide as distance between distals (ns); interrupted by wide, dark or pollenless stripe at least as broad as distance between distals (ws). Specimens should be observed in posterior dorsal view to show maximum extent of pale pollen.

28. Lateral marginals are same as "lateral bristles" of some authors. Ventral marginals include bristles on tergum ventral to laterals.

29. Pale pollen on third abdominal tergum: extending posteriorly to margin between median marginals (ex); not extending posteriorly between median marginals, but small marginal spot not connected with pale basal fascia may be present (ne).

32. Dark fascia on 4th tergum: absent (a); or extending basally from median apical margin of the tergum 1/2, 2/3, 3/4, or 4/4 distance to basal margin (abbreviated 1, 2, 3, 4 respectively). The entire surface of tergum should be observed from behind to determine maximum contrast between white pollen and dark fascia.

34. Body length is measured from anterior surface of third antennal segment (when it is in normal position close against surface of head) to most posterior part of abdomen (not to end of larvipositor or most posterior part of abdomen in a morphological sense).

36. Total number of specimens and number of types examined by present author are listed in detail under discussions of each species. The number of specimens is given in parentheses and refers to females unless males are indicated. All specimens were taken

on Barro Colorado Island, and details concerning their collection are given in a list of all field numbers at the end of the species discussions.

Calodexia van der Wulp

Calodexia van der Wulp (1891: 257). Brauer and Bergenstamm (1891: 375-376, 1893: 130-131), diagnosis. Coquillett (1910: 517), *C. majuscula* designated as type species. Townsend (1927: 219), key. Curran (1934a: 2-3), diagnosis. Curran (in Curran, et al. 1934: 505-506), diagnosis. Curran (1934b: 432, 439, 461), key, figures of head, wing.

Oestrogaster Townsend (1912: 310; 1914: 28). Townsend (1927: 223), key. Aldrich (1929: 21).

Oestrogastropsis Townsend (1915: 424). Townsend (1927: 223), key. Aldrich (1929: 21).

Oestrogastrodes Townsend (1915: 425). Townsend (1927: 225), key. Aldrich (1929: 21).

The generic diagnosis given by Curran (1934a: 2-3) is considered to be correct except for the following modifications.

Occiput with white or yellowish pile and black, white, or yellowish pollen; row of black occipital bristles extends downward at least half length of eye. Cheek at narrowest point 1/7th to 1/15th as wide as height of eye (= maximum length of eye); ocellars short and weak; outer verticals present in females, may be absent in males; palpus with parallel sides or slightly enlarged at apex and with rounded or bluntly pointed tip, some males with apex of palpus swolled to form ovoid club; prementum about twice as long as wide in lateral view. Dorsocentrals 2-3, rarely 3-3; acrosticals usually 1-1, sometimes 0-0, 0-1, 1-3, 2-1, 2-3, 3-1, 3-3, rarely 0-2, 1-2, 2-1, or 2-2, one or more pairs often weak; no presutural intra-alar (= posterior sublateral); anterior intra-alar often weak but rarely absent; presutural present. Middle of propleuron bare; mesopleuron and sternopleuron with fine white, yellowish, or coarser black hairs. Scutellum with two to four pairs of marginals; first pair strong; last pair, located on posterior lateral angle of scutellum, also strong; intermediate pair(s) weak or absent; in addition, a weak or strong apical pair or rarely two weak apical pairs may be present; pollen of scutellum usually dark basally, light at apex, but sometimes entirely light or dark. Squama white, often with faint brown or pale yellow-brown tinge in center or on most of posterior lobe; infrasquamal setulae usually present and black, sometimes absent or yellow. Middle femur with two, occasionally one or three, anterior bristles near middle. Males often with dense row of yellow hairs along inner ventral margin of hind femur, sometimes with rows on both inner and outer margins or no distinct row. Middle tibia usually with one ventral bristle near middle, sometimes a second shorter bristle or no ventral bristle near middle; anterior tibiae with one posterior bristle near middle. Abdomen black, often partially yellow, orange, or reddish and with pale pollen; second and third terga of most species each with basal band of whitish pollen which widens medially; first and second abdominal terga each with a pair of median marginals and a pair of lateral marginals, sometimes with weak row of lateral marginals; third tergum usually with one pair of discals, occasionally one row of four or more; fourth tergum without discals or with one or two rows or a pair.

Key to Species of Calodexia

(Modified from that in Curran [1934a: 3-4].)

1\. Occipital pollen mostly black..................................2.

Occipital pollen mostly white or yellowish.................3.

2 (1). Acrosticals 3-1 or 2-1; pale pollinose fascia on second tergum broadly interrupted in middle; one pair of median marginals and one or more pairs of lateral and ventral marginals on second tergum....................<u>fumosa</u> Townsend.

Acrosticals 1-1; pale pollinose fascia on second tergum entire; continuous row of marginals along entire edge of second tergum............................<u>aldrichi</u> Curran.

3 (1). Without acrostical bristles.................................4.

At least one pair of acrostical bristles....................5.

4 (3). Posterior femora orange basally; median postsutural dark mesothoracic vittae separated by light vitta (seen with light striking the thorax from posterior angle)...<u>fulvibasis</u> Curran.

Posterior femora entirely brownish-black; median dark vittae united behind suture by dark pollen.....<u>townsendi</u> Curran.

5 (3). At least one pair of presutural acrosticals................6.

Without presutural acrosticals..................<u>dives</u> Curran.

6 (5). Three pairs of postsutural acrosticals.....................7.

One pair of postsutural acrosticals (occasionally a second weak pair...11.

7 (6). Acrosticals 2-3 or 3-3; median dark vittae united behind suture or dark fascia across center of entire mesoscutum

except just above wings.....................................8.

Acrosticals 1-3; median dark postsutural vittae separated for entire length by light pollen...............varia Curran.

8 (7). Third tergum with four discals; acrosticals 2-3...mexicana Townsend.

Third tergum with two discals; acrosticals 2-3 or 3-3.......9.

9 (8). Outer dark vittae fused with median dark vitta behind suture; acrosticals 3-3; body length about 8 mm.....valera Curran.

Outer dark vittae separated from median dark vitta by outer light vittae behind suture; acrosticals 2-3, rarely 3-3; body length 4 to 5.5 mm., rarely as large as 7 mm.....10.

10 (9,23). Scutellum with reddish-brown pollen confined to basal dark band; third antennal segment with basal orange color extending distally beyond insertion of arista at least as far as distance from arista to base of third segment...........................panamensis Curran.

Scutellum with reddish-brown pollen over entire dorsal surface except for narrow posterior and lateral margins; third antennal segment orange from base to arista...........................bequaerti Curran.

11 (6). Middle tibia with one or two strong ventral bristles near or beyond the middle....................................12.

Middle tibia without ventral bristle near middle...fasciata Curran.

12 (11). Posterior femora, when seen in ventral view, orange on at least basal fourth, abruptly becoming orange-brown to black distally and with apices usually orange; or entire

femora light yellow to orange in ventral view..........13.

Posterior femora entirely brown to black with no abrupt change in color, the apices sometimes orange or reddish.......20.

13 (12). Infrasquamal cilia black or absent..........................14.

Infrasquamal cilia yellow..............majuscula van der Wulp.

14 (13). Median pale mesonotal vitta extends to well behind suture...15.

Median light mesonotal vitta absent immediately behind suture (when light strikes thorax from posterior angle).......16.

15 (14). Male with a row of yellow cilia on both inner and outer ventral edges of posterior femur for at least distal half; female unknown...................................flavipes Shiner.

Male with a row of yellowish cilia only on inner ventral edge of posterior femur for at least distal half; both sexes with front coxae yellow-orange; sternopleural and lower mesopleural pile light yellowish to brown; female abdomen dorsally black with bluish-white pollen..major Curran.

16 (14). Pile of sternopleura and lower anterior mesopleura fine and white..17.

Pile of sternopleura and lower anterior mesopleura rather coarse and black.......................................18.

17 (16). First abdominal tergum orange with median longitudinal black stripe in female, with weak stripe or no stripe in male...venteris Curran.

Dorsum of first tergum all black.............similis Townsend.

18 (16). Outer light vittae absent behind suture or no wider than half width of outer dark vittae; fourth tergum with 2 to 4

discals...19.

Outer postsutural light vittae as wide as outer dark vittae; fourth tergum with 6 to 10 discals..........agilis Curran.

19 (18). Scutellum with three pairs of lateral marginals; fourth tergum with arched row of four discals...........insolita Curran.

Scutellum with two pairs of lateral marginals; fourth tergum with pair of discals (occasionally a marginal pair may look like a second pair)................apicalis Curran.

20 (12). Sternopleura and lower mesopleura with fine whitish hair; outer dark vittae separated from median dark vitta by light vittae behind suture.................................21.

Sternopleura and lower mesopleura with coarser black hair; all dark vittae united behind suture or outer dark vittae separated from median dark vitta by light vittae.......23.

21 (20). Middle femur with two anterior bristles near middle; dorsum of first tergum black, may be yellow-brown dorsolaterally in male...22.

Middle femur with one anterior bristle near middle; first tergum orange with median dark stripe; female unknown..... ....caudata Curran.

22 (21). Anterior coxae with total of about 35 (range 20 to 50) coarse black hairs and bristles and a few or no fine white hairs; third abdominal tergum of female with pale pollen extending to margin between marginal bristles............... ....interrupta Curran.

Anterior coxae with total of about 12 (range 10-18) black hairs and bristles and numerous fine white hairs; third abdominal tergum of female with pale pollen not extending to margin between marginal bristles but small marginal spot of pale pollen may be present.continua Curran.

23 (20). All dark vittae united behind suture.............bella Curran.

Outer light vittae present behind suture (will key out above through couplet seven if all postsutural acrosticals are visible)..10.

Calodexia agilis Curran

C. agilis Curran (1934a: 13).

A large species (length 5.5 to 8.2 mm.) having a bluish to black abdomen without strong yellowish fascia, the mesonotum with broad postsutural outer light vittae and fused postsutural median dark vittae; the acrosticals 1-1; and the hind femora with orange bases.

Male. Unknown.

Female. Front slightly more than half as wide as eye. Ocellars usually weak, occasionally may be absent. Third antennal segment orange occasionally with browner tinge at apex. Occipital cilia extend down side of head at least two-thirds and usually three-fourths length of eye. Prementum brownish-orange to yellow-brown.

Postsutural outer dark vittae separated from median dark vitta by light vittae about equal in width to outer dark vittae; often these light vittae are narrowed to half width of outer dark vittae near second postsutural dorsocentral. Dorsum of scutellum with basal black band and three or rarely four pairs of lateral marginals. Mesopleural hairs black, sternopleural hairs black with an occasional yellowish hair, pteropleural hairs mostly yellowish. Anterior surfaces of front coxae orange laterally, orange-brown medially; trochanters orange. Front tibiae with three to eight anterodorsal bristles; middle femur usually with two anterior bristles but sometimes one or three; posterior femora usually orange on ventral two-thirds, occasionally entirely orange ventrally.

Third tergum with light pollen extending to apex when seen in dorsal view with specimen rotated to show maximum extent of light pollen. Fourth tergum orange-brown to black in center, usually with dark vertical fascia on distal one-half to two-thirds; when dark fascia is missing entire fourth tergum is covered with white pollen; two or more bristles and numerous hairs along margin next to genital opening.

Records. Barro Colorado Island, 2 ♀ in type series (not seen). Additional records for 286 ♀: over swarm of *Eciton vagans*: 2110 (4); over swarm raid or near *E. burchelli*: 834 (2), 991 (2), 1171 (1), 1172 (5), 1178 (2), 1411 (1), 1412 (2), 1413 (3), 1414 (11), 1415 (2), 1574 (3), 1755 (4), 1757 (5), 1778 (1), 1782 (10), 1784 (3), 1790 (2), 1849 (18), 1854 (1), 1860 (12), 2191 (6), 2230 (34), 2258-X (4), 2293 (2), 2302 (24), 2329 (18), 2341 (16); over swarm raids of *Labidus praedator*: 1277 (17), 1446 (17), 1575 (5), 1617 (2), 2068 (2), 2155 (13), 2156 (1), 2178 (5), 2179 (2), 2201 (1), 2202 (2), 2242 (14), 2257 (6); taken in laboratory: 2254-X (1).

Calodexia aldrichi Curran

C. aldrichi Curran (1934a: 4).

A small species with black occipital pollen as in *C. fumosa*. Characters for separating these two species are given under *fumosa*.

Records. BRASIL: Chapada, ♀ holotype only specimen known (not seen).

Calodexia apicalis Curran

C. apicalis Curran (1934a: 17).

Differs from all other *Calodexia*, when seen in dorsal view, by the broad complete black fascia behind the mesonotal suture, the bluish to black abdomen without strong yellowish fascia, the two pairs of marginal scutellars, and the single pair of discals on the fourth tergum (possibly second weaker pair close to margin).

Male. Not seen, but following changes and additions to Curran's description probably apply also to male, with possible exception of abdominal characters.

Female. Occipital pile white, black occipital cilia extend down side of head half to two-thirds length of eye. Prementum yellow-brown. Second tergum with pale pollen occupying basal three-fourths near ventral edge, narrowing to one-half laterally, narrowing to basal one-third laterodorsally, and widening to three-fourths middorsally. Third tergum with similar but slightly broader pattern of light pollen. Fourth tergum with median shining dark fascia about one-third width of tergum, as seen from below; fascia extends from base to apex and continues more narrowly along margin of tergum.

Records. Barro Colorado Island, 2♂,1♀ in type series (not seen). Additional records for 2♀: over swarm raids of *praedator*: 1446 (1), 2155 (1).

Calodexia bella Curran

C. bella Curran (1934a: 8).

This species is close to *fasciata* but readily distinguished by the following characters (alternatives for *fasciata* in parentheses): when seen in posterior view and posterior light, the postsutural dark fascia is narrowly continued to the wings just behind the mesonotal suture (completely interrupted above wings); there is one midventral bristle on the middle tibia (bristle lacking); there is a shining, broad, median dark fascia on the fourth tergum from base to apex (weak fascia on median posterior area of tergum and dense pale pollen basally).

C. bella was described from 13 males collected on Barro Colorado Island, and Curran (1934a: 9) suggested it might be the male of *C. fasciata*, represented in his collections by 29 females but no males. His suggestion was based largely on the dark mesonotal markings and the relative abundance of these two species. However, we found 56 females which are much closer to *C. bella* than they are to *fasciata*. Important ways in which these females differ from the male are given below. The male of *fasciata* is still unknown.

Male. Legs mostly brown with yellow to orange trochanters and orange areas on coxae. First tergum with irregular dorsolateral brownish yellow spots blending to dark brown or black in middorsum. First and second terga each with narrow yellowish band along ventrolateral margin; second tergum (ignoring pollen) with basal one-half to two-thirds pale brownish yellow to brownish orange, brown on distal third, expanding at least to distal half middorsally where exact extent obscured by dense pollen. Third tergum similar, but brown on distal one-half to three-fourths laterally and ventrally, expanding to basal margin middorsally. Fourth tergum entirely brown; dark vitta, about one-third width of dorsum, extends to basal margin; one strong pair of discals and possibly one or two weak pairs, all in straight line or slightly arched row.

Female. Main differences from male: Head with pollen white to yellowish dorsally and in all areas whiter than in male. Front widest in center, becoming slightly narrower towards antennae and vertex.

Abdomen mostly black. First tergum black dorsally, becoming brown at ventral edge; ventrolaterally with slight trace of whitish pollen. Second tergum dark brown dorsally and lighter brown ventrolaterally; basal band of white pollen extends entire length of tergum near ventral edge, narrowing laterally to about basal half; in dorsal view white pollen narrows to about basal one-third widenning medially to basal one-half to two-thirds. Third tergum similar to second but in dorsal view white pollen on basal one-third to one-half and with its posterior edge almost straight and even with discal bristles. Fourth tergum with strong median pair and usually two weaker lateral pairs of discals arranged in an arched row; discals number from three to eight and vary greatly in size and position.

Records. Barro Colorado Island, 13♂ in type series, 3 paratypes examined. Additional records for 1♂ and 55♀: over swarm raids or near E. burchelli: 827 (6), 834 (12), 944 (1), 991 (2), 1170 (1), 1172 (1), 1411 (1), 1413 (1), 1414 (2), 1574 (2), 1755 (4), 1757 (3), 1784 (1), 1790 (1), 1849 (2), 2293 (2), 2302 (7); over swarm raids of L. praedator 1277 (1), 1446 (1), 1575 (1), 1617 (1), 2155 (1); sweeping on vegetation in forest: 2216 (1♂).

Calodexia bequaerti Curran

C. bequaerti Curran (1934a: 19)

This species is extremely close to panamensis and distinguishing characteristics are given under that species.

Male. Unknown.

Female. Corrections and additions to Curran's description follow based on examination of the holotype.

Front narrowest at bases of antennae and at that point slightly wider than width of eye. Vertex with grey-white pollen tinged with reddish brown near ocelli. Occipital pile white to yellowish. Palpus with less than ten black hairs. Third antennal segment orange from base to insertion of arista, dark brown distal to insertion of arista.

Presutural median dark vittae near nesonotal suture, about equal in width to presutural outer light vittae. Dorsum of scutellum with reddish brown or rust-colored pollen in center, or for entire dorsal surface except for margin when seen from a low anterior angle. Margin of scutellum posterior to first marginal bristles with grey-white pollen tinged with yellow. Three pairs of marginal scutellar bristles and one apical pair which is weaker than marginal scutellars but stronger than most dorsal scutellar hairs. Only one pair of postsutural acrosticals can be seen because of pin; apparently three pairs of postsutural acrosticals can be seen on one or both paratypes.

Legs brown but front trochanters and distal parts of front coxa somewhat lighter yellow-brown. Posterior lobe of squama light yellow-brown, becoming lighter toward outer edge and white at anterior base; anterior lobe white.

All terga brownish black dorsally, becoming brown ventrally. Narrow apical margins of first, second, and part of third terga yellowish ventrally. Pollen on second tergum extending in a blunt point between marginals but not reaching apex of tergum. Third segment with similar pattern. Both second and third terga may appear to have a weak median band of pale pollen extending to apex when seen at a very low posterior angle almost parallel with terga. Fourth tergum with slightly yellowish grey-white pollen on entire surface when seen in oblique dorsal view; when seen from side, tergum has two median dorso-ventral stripes of light pollen which are attenuated to fine points at apex of tergum; highly arched row of nine discals and second row of three discals near middle of tergum; about half of discals hairlike.

Records. Guatemala: 3♀ in type series, holotype examined.

Calodexia caudata Curran

C. caudata Curran (1934a: 16).

Although this species resembles similis, the first and second terga are orange (compared to brown or black in similis). C. caudata is also similar to venteris, but has brownish hind femora, and the head has dense white pollen (compared with yellow to light orange hind femora and gold pollen on dorsal areas of the head in venteris).

Records. PANAMA: Cabima, 1♂ holotype (not seen).

Calodexia continua Curran

C. continua Curran (1934a: 10).

C. continua can be distinguished from interrupta, the most similar species, by the numerous white hairs and the 10 to 18 black hairs and bristles on the anterior surface of the front coxa; the third tergum which has a pale band of pollen not extending to the apex between the median marginal bristles; and the middle tibia which usually has two ventral bristles near the middle.

Female. Front more than half as wide as eye. Black occipital cilia extend down side of head at least one-half and usually two-thirds length of eye. Prementum orange to brown. Palpus orange to yellow-brown. Third antennal segment orange at base, becoming orange-brown at apex.

Outer dark vittae continued to anterior face of thorax but usually narrowed beyond median sublaterals. Median dark vittae fused behind suture. Postsutural outer dark vittae separated from median dark vitta by narrow pale vittae about one-fourth as wide as outer dark vittae. Postsutural outer light vittae often reduced or incomplete near middle postsutural dorsocentrals. Anterior surface of front coxa orange to brown, with numerous long, fine, white hairs and total of 10 to 18 black hairs and bristles. Middle tibia with one long ventral bristle shortly beyond middle and usually one shorter bristle closer to middle.

First tergum with ventrolateral white pollen about as dense as ventrolateral pollen on second tergum. Third tergum with pale pollen extending at most about half way from discals to apex, small marginal spot of pale pollen may be present but not continuous with basal light pollen. Fourth tergum with eight to ten discals in highly arched row and occasionally additional weak discals. Fourth tergum has vertical fascia without pale pollen; color of tergum usually orange, occasionally all brown.

Records. Type series of 16♀: Barro Colorado Island, 14♀; CANAL ZONE: Cano Saddle, 1♀; and GUATEMALA, 1♀. Three paratypes from Barro Colorado Island examined (1♀ paratype, 5812; in Snow Entomological Museum, University of Kansas). Additional records for 119♀: over swarm raids or near *E. burchelli*: 834 (3), 991 (1), 1171 (1), 1172 (1), 1178 (2), 1411 (1), 1412 (2), 1413 (2), 1414 (3), 1415 (1), 1574 (6), 1755 (5), 1757 (11), 1782 (4), 1784 (2), 1790 (5), 1849 (13), 1860 (2), 2191 (3), 2230 (7), 2258-X (1), 2293 (2), 2302 (4), 2341 (3); over swarm raids of *praedator*: 1277 (18), 1446 (10), 1617 (4), 2242 (2).

Calodexia dives Curran

C. dives Curran (1934a: 6).

The large size (6.0 to 9.0 mm.), bluish black abdomen, median dark vittae fused behind the suture, completely dark femora, white hairs on front coxae and most of pleura, and lack of presutural acrosticals separate this species from all other *Calodexia*.

Male. Unknown.

Female. Front more than one-half as wide and usually about three-fourths as wide as eye. Black occipital bristles extend down side of head about two-thirds length of eye. Third antennal segment orange, becoming orange-brown or brown at apex.

Median dark vittae united into single vitta behind suture, but few spots of light pollen occasionally present in center of this vitta. Behind suture outer light vittae about one-half as wide as outer dark vittae. Outer dark vittae continued to anterior surface of thorax but usually narrowed in front of median sublaterals. Scutellum with three, or occasionally four, pairs of lateral marginals; apical marginals absent, hair-like, or strong (but never as strong as posterior laterals). Front coxa orange to orange-brown, with fine white to yellowish hairs and 10 to 18 black hairs and bristles.

Third tergum with pale pollen extending to apex between median marginal bristles, except in a few specimens. Fourth tergum with arched row of 6 to 12 discals; entire surface covered with whitish pollen when seen from posterior dorsal view; when observed perpendicularly to surface of tergum only lateral basal areas show dense whitish pollen.

Records. Barro Colorado Island, 20♀ in type series (none seen). Additional records for 198♀: near _E. burchelli_ or over its swarm raids: 834 (3), 1171 (1), 1172 (1), 1411 (3), 1412 (3), 1413 (9), 1414 (14), 1415 (5), 1755 (7), 1756 (1), 1757 (2), 1782 (2), 1790 (2), 1849 (4), 2230 (2), 2341 (1); over swarm raids of _L. praedator_: 1277 (28), 1446 (68), 1575 (18), 1671 (6), 2068 (3), 2155(7), 2178 (1), 2201 (1), 2242 (4), 2257 (2).

Calodexia fasciata Curran

C. fasciata Curran (1934a: 5).

This species can be distinguished from all other _Calodexia_ by the white occipital pollen, the lack of ventral bristles near the middle of the middle tibia, and the postsutural dark fascia which is completely interrupted above the wings when seen in posterior view with posterior light. (In the most similar species, _bella_, this fascia is narrowly continued to the wings just behind the mesonotal suture.) The fourth tergum, from the margin at the posterior end of the opening for the larvipositor to the median basal margin, is about twice as long as broad and has dense yellowish pollen between the discals and the basal margin. (In *bella*, this same area of the fourth tergum is slightly broader than long, and the shining, dark fascia extends to the median basal margin.)

Male. Unknown.

Female. Front slightly more than one-half as wide as width of eye. Black occipital cilia extending down side of head one-half to three-fourths length of eye.

Weak outer light vittae sometimes partially separate postsutural median dark vitta from outer dark vittae. Dorsocentrals 2-3, occasionally 3-3. Acrosticals 1-1, in addition occasionally one or two weaker presutural pairs and one weaker postsutural pair. Front coxae orange to dark brown. Hind femur, seen ventrally, with basal one-fourth to one-third orange, occasionally entire femur orange to orange-brown.

First tergum orange-brown to black; first and second terga each with one strong pair and usually one or more weaker lateral pairs of marginals. Dorsum of third tergum with posterior edge of pale pollen approximately straight. Fourth tergum about twice as long as broad, with high narrow arch of 7 to 14 discals, some frequently scattered outside row or in second row; color of tergum from orange to yellow-brown to black; dense pale pollen along basal margin but less dense within row of discals.

Records. Barro Colorado Island, 29♀ in type series (none seen). Additional records for 244♀: over swarm of *E. vagans*: 2110 (1); over swarm raids of *E. burchelli*: 367 (2), 827 (3), 834 (28), 944 (2), 1170 (1), 1171 (4), 1172 (3), 1178 (19), 1411 (4), 1412 (3), 1413 (4), 1414 (6), 1415 (1), 1570 (1), 1574 (3), 1755 (21), 1757 (6), 1782 (9), 1784

(7), 1790 (7), 1849 (20), 1860 (1), 2191 (1), 2230 (14), 2293 (1), 2302 (11), 2329 (1), 2341 (7); over swarm raids of L. praedator: 1277 (9), 1446 (12), 1575 (5), 1617 (10), 2068 (1), 2155 (3), 2178 (2), 2242 (3), 2257 (8).

Calodexia flavipes (Schiner)

Meigenia flavipes Schiner (1868: 326)♂.

Calodexia flavipes, Brauer and Bergenstamm (1891: 376). Aldrich (1929: 22-23) redescription of ♂; ♀ = Calodexia varia.

This species is similar to major which may be synonym of flavipes as explained under major.

Records. BRASIL, Novara Expedition, exact locality unknown, 1♀.

Calodexia fulvibasis Curran

C. fulvibasis Curran (1934a: 7) ♀.

Calodexia townsendi and C. fulvibasis are the only two species in the genus lacking all acrosticals. The latter species can be distinguished from townsendi by the median dark vittae which are separated for their entire length; the orange bases of the posterior femora; and the four discals on the fourth tergum.

Records. PERU: Jaen Province: Huascaray Ridge: 7000 feet, 1♀ (not seen).

Calodexia fumosa (Townsend)

Oestrogaster fumosus Townsend (1912: 310). Townsend (1914: 28), correction of description.

Calodexia fumosa, Aldrich (1929: 21), Curran (1934a: 5).

Both *C. aldrichi* and *fumosa* have black occipital pollen and a large dark fascia across the entire thorax behind the suture. These two species can be separated by the following characters (the alternatives for *aldrichi* in parentheses): the band of pale pollen on the second tergum is broadly interrupted in the middle (not interrupted); the second tergum has a pair of median marginals (row of marginals); and the acrosticals are arranged 3-1 or 2-1 (1-1).

The specimens from Barro Colorado Island reported by Curran and my specimens from the same locality, which have been partially determined by him, apparently belong to the same species. However, slight differences in size, color, and morphology may indicate that the Panamanian specimens are not *fumosa*, but a new species.

Male. Unknown.

Female. Not redescribed by Curran. Specimens examined differ from original description in following manner: seven to nine pairs of frontal bristles including two proclinate and two reclinate fronto-orbital pairs in line with frontals; ocellar bristles fine and hair-like; palpi yellow with few short black hairs; antennae yellow to brown. Scutellum with two or usually three marginals. Second abdominal segment with one pair of discals.

Records. PERU: Jaen Province: 5000 feet; on foliage, holotype ♀ (not seen). Barro Colorado Island, 21♀ reported by Curran (1934a: 5); additional records for 85♀: over swarm raids of *E. burchelli*: 827 (2), 834 (3), 1172 (2), 1178 (4), 1411 (1), 1412 (2), 1574 (3), 1755 (1), 1782 (1), 1790 (1), 1849 (1), 2230 (3); over swarm raids of *L. praedator*: 1277 (29), 1446 (10), 1575 (6), 1617 (4), 2155 (1), 2178 (3), 2201 (1), 2202 (1), 2242 (2), 2257 (4).

Calodexia insolita Curran

C. insolita Curran (1934a: 4, 15), key. Curran (in Curran, et al. /1934: 506/).

Although close to apicalis, this species can be separated by the scutellum which has three pairs of lateral marginals, and the fourth tergum which has an arched row of four discal bristles. (The latter is not a generic character as stated in Curran, et al. /1934: 506/).

Records. BRITISH GUIANA: Kartabo, holotype ♀ (not seen).

Calodexia interrupta Curran

C. interrupta Curran (1934a: 9).

This species is similar to continua but easily distinguished from it by the pale pollen extending to the apex of the third tergum between the median marginals. (In continua the pale pollen does not extend medially to the apex, but a small marginal spot of light pollen is sometimes present and not connected with the basal band.) The pleural pile is white, and the anterior surface of each front coxa has a few white hairs and 25 to 35 black hairs and bristles.

Male. Front, at narrowest point near its center, slightly less than half as wide as eye and widening at bases of antennae to more than two-thirds as wide as eye. No proclinate orbitals; ten pairs of frontals including two upper reclinate fronto-orbital pairs. Black occipital cilia extending down side of head two-thirds length of eye.

Outer and inner dark vittae usually at least partially interrupted at suture. Front coxae brown with some brownish orange laterally; hind femora entirely brown to black except for tips, which are somewhat orange. Middle and hind femora each with row of long golden-brown hairs along outer two-thirds of posterior ventral margins; similar shorter row along anterior ventral margin of hind femur. Third tergum with pale pollen usually extending as a narrow band between median marginals to apex. Fourth tergum with curved row of seven to eight discals approximately parallel with posterior edge of second tergum.

Female. Lower two-thirds of front with parallel sides and about two-thirds as wide as eye; front narrowed toward vertex but remaining more than one-half as wide as eye. Two pairs of proclinate orbitals; six to eight pairs of frontals. Apical scutellar bristles hairlike or absent. Middle femur with usually two (occasionally one or three) anterior bristles near middle. Middle tibia with one very rarely two, ventral bristles near middle. Third tergum with basal band of light pollen expanded medially to apex; between median marginals pale pollen at least half as wide as distance between marginals. Fourth tergum with dense whitish pollen along basal margin; dark fascia extending from distal margin of tergum one-half to three-fourths distance to base; discals scattered or arranged in one very irregular row of 8 to 12 bristles.

Records. Barro Colorado Island, 2♂ and 15♀ in type series; 1♂ 3♀ paratypes examined (1♀ paratype, 5813, in Snow Entomological Museum, University of Kansas). Additional records for 6♂ and 170♀: over swarm of E. vagans: 2110 (5♀, 1♂); near E. burchelli or its swarm raids: 834 (4), 991 (1), 1178 (2), 1413 (1), 1414 (1), 1574 (1), 1755 (3), 1757 (2), 1782 (7), 1790 (3), 1849 (6), 1860 (15), 2191 (8), 2230 (17), 2258-X (2), 2302 (6), 2329 (11), 2331 (1), 2341 (14); over swarm raids of L. praedator: 1277 (5), 1446 (4), 1575 (1), 1617 (12), 2068 (1), 2155 (1), 2178 (9), 2179 (4), 2201 (10), 2202 (2), 2206 (1), 2242 (4), 2257 (1); reared from cricket escaping from swarm raid of E. burchelli: 2260-X (4♂, 4♀); taken in laboratory: 1552 (1), 2346 (1♂).

Calodexia major Curran

C. major Curran (1934a: 12)♂ ♀.

This is one of the larger species (6.8 to 8.9 mm). The hind femur has at least the basal half orange, and the postsutural median dark vittae are separated by light pollen. The female has a bluish black abdomen and the third tergum has pale pollen extending from the median marginals to the apex. The males have reddish first and second terga.

The males according to Curran (1934a: 3, 11-12) also have a single row of long yellow cilia along almost entire length of the posterior ventral margin of each hind femur. The two male specimens examined have a weaker row of the same type hairs along the distal one-fourth to one-third of the anterior ventral margin of the hind femur. The presence of a single row of ventral cilia on the hind femur of the male is the only character used by Curran to separate C. flavipes Schiner from major. Curran did not see the type of flavipes but examined one specimen from the U. S. National Museum which had been compared with the type and was considered to be identical by Aldrich. However, Curran found that that specimen did not agree with the original description of flavipes, and he decided that major was a distinct species. No sound conclusion can be reached on this problem without re-examination of the type of flavipes.

Male. Front narrowest at level of ocelli where 2/7 to 2/9 as wide as eye; width of front doubled at level of antennae. No proclinate fronto-orbitals. Black occipital cilia extending downward two-thirds length of eye.

All mesonotal vittae may be partially interrupted at suture. Apical scutellars hair-like or absent. Sternopleura with yellowish white hairs; mesopleura with yellowish white hairs on central and antero-ventral areas, and dark brown to black hairs along antero-dorsal, dorsal, and posterior margins. Notopleura with dark hairs. Coxae mostly orange with small areas of orange-brown, and with yellowish white and brown or black hairs. Hind femur with one row of long yellow hairs along almost entire length of posterior ventral margin and second weaker row along distal one-fourth to one-third of anterior ventral margin.

First tergum with ventral and lateral areas pale brownish yellow to pale brownish orange; darker brown median stripe continued along apical margin laterally to lateral marginals.

Female. Two proclinate fronto-orbitals and seven to eight pairs of frontals (including two pairs of reclinate fronto-orbitals). Front coxae as given above for male. Middle femur with two or occasionally one anterior bristle near middle. Posterior femur with approximately basal half orange and distal half orange-brown or occasionally with entire femur orange-brown. Hind femora without long yellow ventral cilia.

Fourth tergum with one highly arched row of discals and occasionally second partial row or some scattered bristles outside of main row.

Records. Type series of 3♂, 15♀: Barro Colorado Island, 2♂, 14♀; PANAMA: Gatun Lake: Cano Saddle, 1♀; COSTA RICA: La Suiza, 1♂ (none seen). Additional records for 2♂, 43♀: over swarm raids of E. burchelli: 834 (8), 1141 (1), 1414 (1), 1419 (1), 1574 (1), 1782 (1), 1784 (1), 2191 (1), 2230 (2), 2258-X (2), 2302 (4), 2329 (3), 2341 (3); over swarm raids of *L. praedator*: 1277 (2♀, 1♂), 1446 (5), 1617 (2), 2155 (1♀, 1♂), 2178 (1), 2179 (1), 2201 (1), 2242 (1).

Calodexia majuscula van der Wulp

C. majuscula van der Wulp (1891: 257-258, pl. 6, figs. 12, 12a) ♂; figs. of side of head, dorsal view including wings. Coquillett (1910: 517) designated type species (first of three species described by van der Wulp [1891]). Aldrich (1929: 21-22) redescription based on ♂ which had been compared with type. Curran (1934a: 13).

This species is distinct from all other *Calodexia* since it has pale infrasquamal cilia, and the abdomen is mainly yellow to orange with a strong dark median stripe on both the first and second terga.

The diagnostic character, presence of pale infrasquamal cilia, used to separate this species, is taken from the redescription by Aldrich (1929) based on a specimen which had been compared with the type by Major Austen. The figure of the dorsal view (van der Wulp, 1891: pl. 6, fig. 12) shows a broad pale median vitta behind the mesonotal suture. This may not be present when seen from posterior view with posterior light.

Records. MEXICO: Tabasco: Teapa; ♂ holotype; Morelos: Cuernavaca, 1♂ (Aldrich, 1929) (not seen).

Calodexia mexicana (Townsend)

Oestrogastropsis mexicana Townsend (1915: 424-425) ♀.

Calodexia mexicana, Aldrich (1929: 21). Curran (1934a: 21).

This is a medium to large species with three postsutural acrosticals as in varia and valera. It differs from these two species by having two presutural acrosticals and four discals on third tergum.

There can be little doubt that this is a distinct species. Curran examined the type and separated mexicana in his key by the presence of acrosticals 2-3 (not mentioned by Townsend). The original description will fit almost all species in Calodexia except for the unusual number of four discals on the third tergum.

Records. MEXICO: Veracruz, ♀ holotype (not seen).

Calodexia panamensis Curran

C. panamensis Curran (1934a: 18). ♂♀.

A small species close to bequaerti from which it can be distinguished by the following characters (alternatives for bequaerti in parentheses): The third antennal segment is brown except for some orange near the base. The orange color is continued, on at least the medial side of the segment, to a point at least as far beyond the insertion of the arista as the latter is beyond the base of the segment (the orange color extends only from the base of the third segment to the insertion of the arista). In addition, the vertex has shining yellowish white pollen (duller yellowish grey-white pollen on the vertex with a red-brown tinge near ocelli); the scutellum, when seen in oblique anterior view, has reddish brown or rust-colored pollen confined to a basal dark band (reddish brown pollen over the entire dorsal surface except for the posterior and lateral margins); in perpendicular dorsal view the anterior border of light pollen on the scutellum appears to be straight (anterior border of light pollen concave, parallel to the apical scutellar margin).

In comparing the holotype of <u>bequaerti</u> with my series of <u>panamensis</u> the following characters used by Curran (1934a: 18-19) were found to show no reliable interspecific differences: total length; relative length of outer verticals; color of frontal vittae, squamae, abdomen, and legs; number of marginal scutellar bristles; and patterns of pale pollen on the abdominal terga.

Male. No specimens examined.

Female. Front as wide or slightly wider than either parafrontal; six to nine pairs of frontals; outer verticals more than half as long as verticals.

Apices of first, second, and part of third terga yellowish on ventral surface. Light pollen on second tergum extends in middle from base to median marginal bristles or to apex; pale pollen occupies basal one-half to two-thirds of tergum dorsolaterally, and widens to at least three-fourths at ventral margin. Third tergum with pattern of pollen as in second or with slightly broader band of pale pollen with straighter posterior edge. Fourth tergum with slightly yellowish gray-white pollen on entire surface when seen in oblique dorsal view; when seen from side, tergum has two median dorso-ventral stripes of light pollen which are attenuated to fine points at apex of tergum; about ten discals arranged in highly arched row, and about three additional discals in second row near middle of tergum, occasionally discals in three indistinct rows; about half of discals are hair-like.

Records. Type series of 3♂ and 4♀: Barro Colorado Island, 2♂, 2♀; Canal Zone: Cano Saddle, 2♀, Tabernilla 1♂ (none seen). Additional records for 29♀: over swarm raid of <u>E. burchelli</u>: 1782 (2);

over swarm raids of *L. praedator*: 1277 (3), 1446 (9), 1575 (6), 1617 (2), 2155 (2), 2179 (3), 2242 (1), 2257 (1).

Calodexia similis (Townsend)

Oestrogastrodes similis Townsend (1915: 425) ♀.

Calodexia similis, Aldrich (1929: 21). Curran (1934a: 14).

Although close to *agilis*, *continua*, and *interrupta*, this species can be separated by the white hairs on the pleura together with the bases of the posterior femora appearing orange when seen in ventral view.

These structures, used by Curran (1934a: 14) for separating *similis* from *agilis*, are found in both species or are too variable to be of value: ocellar bristles, anterior dorsal bristles on the front tibiae, and marginal bristles on the fourth torgum.

The male of *similis* is described here for the first time. Because Curran did not redescribe *similis* and Townsend's description is very incomplete, a more complete description of the female is also included.

Male. Head with dense white pollen becoming gold on parafrontals and upper posterior orbits. Background color of cheek (ignoring pollen) orange-brown; parafacials orange becoming brown on front. Sides of front straight and diverging; front narrowest at vertex where slightly wider than half width of eye; at dorsal edges of antennal bases front almost as wide as eye. Frontal vitta dark reddish brown to black and about as wide as parafrontals. Nine pairs of frontals, including two pairs of reclinate fronto-orbitals and two pairs of proclinate fronto-orbitals. Ocellars strong (for *Calodexia*), as long or longer than width of frontal vitta at widest point. Occipital pollen and pile white or slightly yellowish; median and dorsal dark areas in pollen. Black occipital cilia extend downward three-fourths length of eye. Prementum light yellowish brown. Palpus swollen club-like, distal half more than twice diameter of basal half; with more than 25 short black hairs, fewer scattered long yellow hairs, and dense covering of short pale pile merging into pollen basally. Entire antenna dark brown except for lighter brown arista and lighter more orange areas on second segment and base of third segment below arista. Arista with longest dorsal hairs about twice as wide as arista at widest point, ventral hairs shorter than width of arista.

Thorax with white pollen becoming pale yellowish on dorsum. Presutural median dark vittae about three-fourths as wide as presutural outer light vittae. Presutural outer dark vittae more than twice as wide as outer light vittae and extended broadly to anterior surface of thorax. Median dark vittae not interrupted at suture; outer dark vittae interrupted laterally by an indentation of light pollen. Median dark vittae united behind suture into a broad median vitta which narrows in middle of scutum and extends posteriorly as more gray and indistinct narrow median stripe to scutellum. Postsutural outer light vittae about half as wide as outer dark vittae. Scutellum with basal dark band, three pairs of marginal scutellars, and one weak hair-like apical pair. Pile on pleura white except for anterodorsal, dorsal, and posterior margins of mesopleura which have some dark hairs. Notopleuron with about six black hairs. Subsquamal cilia black. Acrosticals 1-1; anterior intra-alar strong.

Anterior surface of front coxa with outer orange band, inner brown band, about 30 to 40 black hairs and bristles, and many thin yellowish hairs. Basal one-half to three-fourths of each middle and hind femur orange in ventral view. Middle femur with two anterior bristles near middle; middle tibia with single ventral bristle somewhat beyond middle. Posterior femur with row of brown hairs along only about distal third of inner posterior margin; at apex of femur these hairs about as long as width of hind tibia, becoming shorter toward base of femur. No yellow cilia on hind femur.

Abdomen black with grey-white ventrolateral pollen becoming tinged with yellow dorsally. First tergum black and with no pale pollen in dorsal view; ventrolaterally with white pollen present but less dense than on same area of second tergum. Second tergum with narrow median dark stripe and dark patches around discals; white pollen bordering stripe for basal two-thirds of tergum, pollinose area narrowing abruptly to less than basal one-fourth on more lateral areas of dorsum, widening to about basal two-thirds at level of lateral bristles, and widening to at least three-fourths ventrally. Third tergum with triangle of whitish pollen extending to apex medially but weak between marginals; when viewed at a low posterior angle, almost parallel to the tergum, a median dark stripe can be seen; laterally pattern of pollen is like that of second tergum. Fourth tergum reddish brown but completely covered with light pollen in most views; slight trace of narrow median dark vitta; one row of four to six discals; second and third terga each with one pair of discals. First and second terga each with one pair of median and one pair of lateral marginals; third and fourth each with a row of marginals. Hairs black, except white on first abdominal sternum (first morphological segment) and ventrolateral areas of first tergum.

Female. Differs from male as follows: pollen on upper parts of head less golden, but more yellowish gray-white. Front narrowest at vertex where almost two-thirds as wide as eye. Front widening in middle, becoming slightly narrower below, and then widening again at bases of antennae; at widest points in middle and at bases of antennae about three-fourths as wide as eye. Frontal vitta one-half as wide as to slightly wider than parafrontals. Nine to 11 pairs of frontals including fronto-orbitals. Black occipital cilia extend downward at least one-half and usually two-thirds length of eye. Prementum orange-brown. Palpus of about equal diameter for entire length. Antenna with basal segments orange to brown; third segment orange for at least basal one-third and brown distally. Longest hairs on arista two to three times width of arista at widest point.

Thorax with presutural median dark vittae equal in width or slightly narrower than presutural outer light vittae. All dark vittae narrowly interrupted at suture. Postsutural median dark vitta not continued to scutellum. Apical scutellars may be absent.

Anterior surface of front coxa with seven to ten black hairs and bristles and many thin white or yellowish hairs. Row of brown hairs on inner posterior margin of hind femur present but sometimes less distinct than in male.

First tergum with traces of light pollen visible in dorsal view; ventrally with white pollen almost equal in density to that on second tergum. Second and third terga without median dark stripes. Light pollen on basal two-thirds of second tergum medially, pollinose area narrowing only slightly to dorso-lateral angle of tergum; ventrally light pollen may occupy basal three-fourths of tergum. Third tergum similar to second of female but with pale pollinous area extending to apex between median marginals. Fourth tergum black, completely pale pollinose, or median dark fascia may occupy distal one-half to two-thirds of tergum; one highly arched row of 9 to 14 discals and sometimes second row of two to three discals. Ventral white hair more numerous than in male and also found on second abdominal tergum.

Records. Type series of 2♀: PANAMA: Arajan /= Prov. Panamá: Arraijan ?/ 1♀; MEXICO: Veracruz: San Rafael: near Jicaltepec, 1♀. PANAMA: Canal Zone: Barro Colorado Island, 2♀, (Curran, 1934a: 14); additional records for 2♂, 107♀: over swarm of E. vagans: 2110 (1); near E. burchelli or its swarm raids: 834 (4), 944 (1), 991 (1), 1170 (1), 1171 (2), 1172 (9), 1178 (1), 1394 (1), 1412 (1), 1413 (8), 1414 (5), 1415 (4), 1574 (4), 1755 (5), 1757 (5), 1782 (4), 1784 (1), 1849 (3), 1860 (2), 2191 (2), 2230 (4), 2302 (4), 2329 (3), 2341 (2); over swarm raids of L. praedator: 1277 (5), 1446 (8), 1575 (3), 1576 (2♂), 1617 (2), 2155 (2), 2178 (1), 2242 (3), 2257 (2); taken in laboratory: 1940 (1).

Calodexia townsendi Curran

C. townsendi Curran (1934a: 7) ♀.

This species lacks all acrosticals like fulvibasis but differs from the latter by having the median dark vittae united behind the mesonotal suture, blackish hind femora, and six discals on the fourth tergum.

Records. PERU: Jaen Province: Huascaray Ridge: 7000 feet, ♀ holotype (not seen).

Calodexia valera Curran

C. valera Curran (1934a: 19) ♂.

Although close to *panamensis* and *varia*, *Calodexia valera* can be easily identified by its having acrosticals 3-3, and by the black mesonotal vittae which are all united behind the suture.

Records. VENEZUELA: Valera, 1 ♂ (not seen).

Calodexia varia Curran

C. flavipes, Aldrich (1929: 23-24) ♀ description, misidentification.

C. varia Curran (1934a: 20).

C. varia is another large species (6.3 to 7.8 mm.) with a bluish abdomen similar to that of *agilis*, *apicalis*, *dives*, *major*, and *similis*. However, it differs from these species by the presence of a median light vitta extending the entire length of the mesonotum; the scutellum lacks a basal dark band, is entirely covered with whitish pollen, and has three pairs of marginal scutellars.

Male. Unknown.

Female. Front narrowest at vertex and almost three-fourths as wide as eye; front only slightly wider in middle; frontal vitta reddish brown to black, slightly narrower to wider than either parafrontal. Third segment of antenna orange at least from base to insertion of arista and sometimes for about basal third, distally orange-brown to dark brown.

Third tergum with at least one pair of median discals, sometimes up to nine discals in transverse row. When four or more discals are present usually a lateral discal pair is present in addition to median discal pair. ("Median discals" are in usual dorsal position and "lateral discals" are same distance from basal margin but on lateral part of tergum directly anterior to lateral marginals.) Fourth tergum has strong row of 6 to 12 discals and may have second distal row of about two bristles.

Records. Barro Colorado Island, 1♀ holotype. COSTA RICA: Higuito, 1♀ described by Aldrich (1929: 23-24) as the female of C. fasciata (neither seen). Additional records for 10♀: over swarm raids of E. burchelli: 1172 (1), 1418 (1), 1755 (1), 2302 (1); over swarm raids of L. praedator: 1277 (1), 1446 (2), 2179 (1), 2201 (1); sweeping on vegetation in forest: 1723 (1).

Calodexia venteris Curran

C. venteris Curran (1934a: 15) ♀.

Only C. majuscula and venteris have a yellow to orange abdomen with a median dark stripe. C. venteris differs from majuscula by having black infrasquamal cilia. In the male all four abdominal terga are orange, the third with a brown marginal stripe composed mainly of dark brown spots at the bases of the marginals. The first tergum of the female is orange with a strong median brown stripe; the second tergum is orange with a wider median brown stripe continued as an apical brown stripe; the third and fourth terga are brown dorsally.

Two males and one female were reared from larvae removed from a Calodexia venteris female and introduced into a puncture made in the abdomen of a cockroach. The male description given below is based on these reared specimens which must belong to venteris unless this species is a complex of several similar species.

Male. Agrees with description of female (Curran, 1934a: 15-16) except as follows: Head with white pollen becoming gold above antennae and on upper occiput; background colors (ignoring pollen): orange on cheek; darker reddish orange and brown on front; and orange-brown, red-brown, or brown on occiput. Front narrowest in middle where about one-fourth as wide as eye; at vertex and bases of antennae one-third to one-half as wide as eye; 10 to 11 pairs of frontals, lower six to nine pairs decussate, remaining upper pairs reclinate. Black occipital cilia extend downward one-half to two-thirds length of eye. Outer verticals less than half as long as verticals and far back on head in line with occipital cilia. Inner verticals decussate or sloping together at tips. Palpus with scattered long fine yellowish hairs, 10 to 30 coarser black hairs, and dense covering of short closely appressed fine yellow hairs. Antenna entirely yellow except for arista which is orange at base and brown to black distally.

Humeri with gold pollen; pollen on upper mesopleura yellowish. Middle marginal scutellar weak or absent. Coxae and femora light yellow to orange and lighter than in female. Coxae with fine white to yellow hair. Middle femur with one anterior bristle near middle; hind femur with row of long yellow cilia on inner ventral margin.

All terga entirely orange except: first may have faint median brown stripe, third has brown spots at bases of marginals which tend to fuse into brown apical stripe. First tergum without pollen; other terga with inconspicuous white pollen ventrally, becoming yellow to gold dorsally. Second tergum with white pollen usually visible only laterally and on less than basal fourth; indistinct wider band of yellow pollen dorsally. Similar band along basal one-half to two-thirds of third tergum, becoming somewhat wider medially. Fourth tergum dorsally with yellow pollen on basal one-half to two-thirds, pollinose area increasing ventrally to apical margin. First and second terga each with pair of median and pair of lateral marginals; third with row of 11 to 12 marginals; fourth tergum with row of 12 marginals; marginals on all four terga of about equal size. Fourth tergum with row of six discals in center of tergum. Genitalia yellow to orange.

Female. Specimens agree with description by Curran except: front about two-thirds as wide as eye. Black occipital cilia extend downward one-half to two-thirds length of eye. Palpus as described above for male. Third segment of antenna yellow to orange with brown color varying from faint apical tinge to brown on distal two-thirds.

Middle femur with two anterior bristles near middle (about two percent of females have one bristle on one or both middle femora).

Pollen on all terga white ventrally, becoming yellow to gold dorsally. In ventral view abdomen appears yellow to reddish orange; apical brown band on second tergum usually does not extend for more than lateral half of ventral surface; apical brown band on third terga wider and usually extends almost to ventral edge. First and second terga each with pair of median and pair of lateral marginals.

Records. Type series of 29♀: Barro Colorado Island, 28♀: COSTA RICA: Higuito, San Mateo, 1♀; (none seen). Additional records for 2♂, 441♀: over swarm of *E. vagans*: 2110 (6); near *E. burchelli* or over its swarm raids: 367 (2), 827 (6), 834 (21), 944 (2), 991 (1), 1170 (16), 1171 (11), 1172 (12), 1178 (15), 1411 (4), 1412 (2), 1413 (3), 1414 (6), 1569-A (1), 1574 (2), 1750 (2), 1755 (14), 1757 (6), 1782 (18), 1784 (4), 1790 (6), 1849 (12), 1854 (4), 1860 (6), 2191 (12), 2230 (54), 2258-X (9), 2302 (40), 2329 (20), 2331 (4), 2341 (30); over swarm raids of *L. praedator*: 1277 (11), 1446 (10), 1575 (5), 1617 (8), 2068 (2), 2155 (10), 2178 (6), 2179 (2), 2201 (7), 2202 (4), 2242 (8), 2257 (16); reared from larvae artificially introduced into cockroach: 2236 (2♂, 1♀).

List of Field Numbers with Collecting Data for Flies

The date, time and other important data are given below for all the flies collected in order to save space in preceding pages. The lists are arranged in order of field number under three main headings for flies associated with (1) *Labidus praedator*, (2) *Eciton burchelli*, (3) other ants or those flies taken which were not associated with any ants. All specimens were collected on Barro Colorado Island, Canal Zone, Panama, by the author and his wife, Marian E. Rettenmeyer, except for specimens with 1952 and 1955 dates which were taken by the author alone. The total number of specimens is given for the three genera discussed in this paper: *Stylogaster* (*S.*), *Calodexia* (*C.*), and *Androeuryops* (*A.*). All field numbers with letters after them (e. g., 2341-A) have the same data in this list as the same numbers without the letter, except for those followed by the letter X which have different data.

Associated with *Labidus praedator*

All specimens were taken over swarm fronts or up to two meters in advance of the ants except where other data are given.

465 - 25 Apr. 1952, 1:00 p.m., 1 *S.*

1277 - 27 Feb. 1956, 1:00 to 2:00 p.m., raid swarm stopped about 1:45

p.m., 5 *S.*, 130 *C.*, 11 *A.*

1446 - 15 Mar. 1956, 1:00 to 1:15 p.m., raid swarm unusually large, more than five meters wide at front, 7 *S.*, 157 *C.*, 6 *A.*

1575 - 27 Mar. 1956, 10:55 to 11:00 a.m., 1 *S.*, 50 *C.*, 8 *A.*

1576 - 27 Mar. 1956, 11:10 to 11:15 a.m., same raid as 1575, but flies seen flying repeatedly over a cockroach; whether larvae were deposited could not be determined; 2 *C.*

1617 - 6 Apr. 1956, 10:55 to 11:05 a.m., 7 *S.*, 53 *C.*, 9 *A.*

2068 - 5 July 1956, 10:30 to 11:00 a.m., 9 *C.*

2155 - 21 July 1956, 12:15 to 1:00 p.m., taken one to two meters in advance of swarm front, 43 *C.*, 7 *A.*

2156 - 21 July 1956, about 12:15 p.m., same raid as 2155, 1 *C.*

2178 - 25 July 1956, 10:00 to 10:15 a.m., 28 *C.*, 1 *A.*

2179 - 25 July 1956, 11:00 to 11:15 a.m., same raid as 2178, 1 *S.*, 13 *C.*

2201 - 27 July 1956, 9:55 to 10:05 a.m., small swarm front only one to two meters wide, field numbers 2202, 2206, 2207 from same raid, 1 *S.*, 22 *C.*, 1 *A.*

2202 - 27 July 1956, 9:55 to 10:05 a.m., 9 *C.*

2206 - 27 July 1956, 11:15 to 11:20 a.m., taken by sweeping over entire area of raid seen from 9:55 to 10:20. Raid swarm stopped at 10:20, but workers continued to tear apart booty and were seen running along raid columns to several holes in the ground up until 11:10. 1 *C.*

2207 - 27 July 1956, 10:10 a.m., taken in copulo on leaf 15 cm. above ground, 2 *A.*

2242 - 31 July 1956, 10:00 to 11:00 a.m., sweeping quite intermittently over swarm, 6 *S.*, 42 *C.*

2257 - 1 Aug. 1956, 1:00 to 1:15 p.m., 40 C., 1 A.

2258 - 1 Aug. 1956, same raid as 2257, may have been in copulo, 2 S.

Associated with *Eciton burchelli*

All specimens were taken over swarm fronts or up to two meters in advance of the ants except where other data are given.

367 - 1 Apr. 1952, 12:30 p.m., 4 C.

827 - 10 Feb. 1955, 10:30 to 10:40 a.m., 17 C., 2 A.

834 - 12 Feb. 1955, 11:30 a.m. to 12:00 noon, colony '55 B-IV with a sexual brood on the first statary day, 88 C., 6 A.

944 - 2 Mar. 1955, 8:10 a.m., 6 C.

991 - 9 Mar. 1955, 10:45 to 11:45 a.m., taken within one meter of bivouac while colony had two columns out one to two meters, 8 C.

1170 - 16 Feb. 1956, 9:45 to 10:15 a.m., same raid as numbers 1171, 1172, 19 C., 36 A.

1171 - 16 Feb. 1956, 10:15 to 10:30 a.m., 22 C., 53 A.

1172 - 16 Feb. 1956, 10:30 to 10:45 a.m., 34 C., 127 A.

1178 - 17 Feb. 1956, 10:15 to 10:30 a.m., 1 S., 45 C., 9 A.

1394 - 7 Mar. 1956, about 11:00 a.m., 1 C.

1411 - 8 Mar. 1956, 10:00 to 10:15 a.m., same raid as numbers 1412 to 1419, a large raid but not maximal, 7 S., 16 C., 7 A.

1412 - 8 Mar. 1956, 10:15 to 10:30 a.m., 4 S., 15 C., 14 A.

1413 - 8 Mar. 1956, 10:30 to 10:45 a.m., 6 S., 31 C., 37 A.

1414 - 8 Mar. 1956, 10:45 to 11:00 a.m., 7 S., 49 C., 32 A.

1415 - 8 Mar. 1956, 11:00 to 11:15 a.m., 6 S., 13 C., 24 A.

1416 to 1419 - 8 Mar. 1956, about 11:00 a.m., 2 S., 2 C.

1569-A - 26 Mar. 1956, about 10:10 a.m., 1 C.

1570 - 26 Mar. 1956, about 10:10 a.m., 1 *C.*

1574 - 27 Mar. 1956, 8:50 to 9:50 a.m., sweeping quite intermittently, 25 *C.*, 14 *A.*

1750 - 10 May 1956, 4:20 to 4:30 p.m., swarm front very weak and never more than 20 cm. wide, 2 *C.*

1755 - 11 May 1956, 9:25 to 9:40 a.m., same raid as 1756, 1 *S.*, 65 *C.*, 14 *A.*

1756 - 11 May 1956, 9:40 to 10:10 a.m., aspirated as flies hovered over or sat within a few centimeters of cluster of ants around a cricket, 1 *C.*

1757 - 11 May 1956, 1:50 to 2:05 p.m., same raid as 1758, 4 *S.*, 40 *C.*, 22 *A.*

1758 - 11 May 1956, between 2:05 and 2:50 p.m., attempted to get more *Stylogaster* specimens and ignored *Calodexia*, 2 *S.*

1778 - 12 May 1956, 6:00 to 6:30 a.m., 1 *C.*, only fly seen.

1782 - 13 May 1956, 11:05 to 11:20 a.m., 58 *C.*, 23 *A.*

1784 - 14 May 1956, 7:50 to 8:05 a.m., swarm front four to five meters wide, 19 *C.*, 17 *A.*

1790 - 15 May 1956, 8:05 to 8:20 a.m., 1 *S.*, 27 *C.*, 20 *A.*

1849 - 25 May 1956, 11:15 to 11:30 a.m., 2 *S.*, 79 *C.*, 9 *A.*

1854 - 26 May 1956, 11:00 a.m., 5 *C.*

1860 - 28 May 1956, 2:40 to 2:55 p.m., 4 *S.*, 38 *C.*, 3 *A.*

2191 - 26 July 1956, 11:25 to 11:50 a.m., 33 *C.*, 1 *A.*

2230 - 30 July 1956, between 9:45 and 11:45 a.m., 4 *S.*, 137 *C.*, 1 *A.*

2258-X - 7 Aug. 1956, 10:45 to 10:55 a.m., 1 *S.*, 18 *C.*

2293 - 10 Aug. 1956, about 9:00 a.m., 7 *C.*

2302 - 11 Aug. 1956, 11:00 to 11:20 a.m., 1 *S.*, 101 *C.*

2329 - 17 Aug. 1956, 11:00 to 11:30, 56 *C.*

2331 - 17 Aug. 1956, 12:00 noon, 5 *C.*

2341 - 18 Aug. 1956, 9:00 to 10:00 a.m., 76 *C.*

Associated with Other Ants or Not Found Near Ants

995 - 10 Mar. 1955, 1:15 p.m., hovering next to bivouac of *E. hamatum*, 6 to 12 cm. over ants on ground next to bivouac, 2 *S.*

1552 - 22 Mar. 1956, taken in laboratory, 1 *C.*

1588-B - 29 Mar. 1956, sweeping, not near ants, 1 *A.*

1666-B - 21 Apr. 1956, sweeping, not near ants, 1 *A.*

1723 - 9 May 1956, sweeping low vegetation in forest not near ants, 1 *C.*

1940 - 7 June 1956, taken in laboratory, 1 *C.*

2110 - 9 July 1956, 11:45 a.m. to 12:15 p.m., sweeping over swarm of workers of *E. vagans* which were milling around the site of a bivouac which I had disturbed. This colony had a brood of male and queen larvae, and the workers may have been more excited because of them. Workers covered the ground densely for only one-fourth to one-third square meter, with less dense ants over two square meters. By 12:15 p.m., when the ants had largely quieted down and retreated underground, most of the flies had disappeared, 3 *S.*, 18 *C.*

2216 - 29 July 1956, sweeping low vegetation in forest not near ants, 1 *C.*

2236 - Reared from cockroach into which larvae from adult fly were introduced through puncture in abdomen, 3 *C.*

2254-X - 4 Aug. 1956, taken in laboratory, 1 *C.*

2260-X - 7 Aug. 1956, 10:50 a.m., cricket taken escaping from swarm raid of E. burchelli; flies emerged 21 to 22 Aug., 8 C.

2346 - 19 Aug. 1956, 9:00 p.m., taken in laboratory, 1 C.

Calliphoridae: Phaenicia purpurescens (Walker)

The only well-substantiated cases of Calliphoridae being associated with Dorylinae are those of Bengalia and similar flies found over swarm raids of African driver ants. These flies will be briefly discussed below under Comparisons Between Flies Associated with American and African Dorylines.

A total of 146 Calliphoridae belonging to six species (determined by Maurice T. James) were taken on Barro Colorado Island during the course of this study. Most of the specimens were reared from or taken near dead mammals; and since the army ants were not present, these calliphorids will not be discussed. However, since one species, Phaenicia purpurescens, was found consistently over swarm raids and at no other time, it could not have been present by chance.

Phaenicia purpurescens (Walker) was repeatedly found over swarm raids of both Labidus praedator and Eciton burchelli. It was never reared from carcasses, and only a single male was taken by sweeping over a dead animal (sloth). According to Hall (1948: 256-257) this species ranges from southern México to Argentina. Regarding the biology of P. purescens, Hall states, "Although the species is well-distributed, it is apparently uncommon or extremely localized where it does occur. Considerable effort was expended in an attempt to collect and study this species in the field, but no specimens were ever seen in nearly a year's collecting. The immature stages are unknown."

A total of 20 females and 14 males were taken by sweeping over the swarm raids and up to two meters in advance of the swarm fronts. Four additional females were taken by sweeping vegetation close to the ground in the forest. The flies were taken between January and August during 1952, 1955 and 1956; and the small number of records does not indicate any seasonal fluctuation.

A total of ten males and 17 females were taken near swarm raids of burchelli, three males and three females were taken near swarm raids of praedator, and one male was taken near vagans. Perhaps these flies were attracted by the large number of other flies flying over the swarm. Nothing was noticed about their behavior which gave any clue as to whether or not their host or life cycle is associated with the army ants.

Records. Dates and other details for the following records can be found above in the List of Field Numbers with Collecting Data for Flies. Barro Colorado Island, over swarm of E. vagans: 2110 (1♂); over swarm raid of E. burchelli: 827 (1♀), 834 (1♀), 1172 (1♀), 1178 (1♀), 1277 (1♀), 1411 (1♀), 1413 (1♂), 1414 (1♀), 1574 (1♂, 2♀), 1755 (1♂, 3♀), 1757 (1♀), 1782 (3♂), 1784 (1♀), 1790 (1♂, 1♀), 1849 (2♂), 2329 (1♀), 2331 (1♂), 2341 (1♀); over swarm raids of L. praedator: 2155 (1♀), 2178 (1♂, 2♀), 2179 (1♂), 2257 (1♂).

Sarcophagidae

Approximately 180 Sarcophagidae were taken by sweeping over the swarm raids of army ants on Barro Colorado Island, and almost all these flies belong to new species (determined by H. R. Dodge). Although some of these may have been found there by chance and have no association with the Ecitonini, the biology of other species probably is closely connected with that of the ants. No previous records of Sarcophagidae associated with Ecitonini are known to me. On the basis of the few observations recorded below, it seems safe to construe that perhaps 20 species of sarcophagids are associated with the army ants. There is the possibility that some of these flies, especially the males, may have been attracted by the presence of the hundreds of other flies buzzing around the swarm fronts. However, the fact that females as well as males were present strengthens the possibility that the life cycles of the four important genera discussed below are connected with the biology of the ants. Moreover, specimens of Sarcophagidae collected by sweeping areas where no army ants were raiding, by and large, are feeders on vertebrate carcasses and have been previously described. It is unlikely that any difference in the ecology of the areas would contribute to the marked divergence of species taken because the areas were in adjacent parts of the same forest and in some cases were the identical places swept on different days, both while the army ants were raiding and before or after the raids.

The genera most likely associated with the army ants will be discussed first in alphabetical order, and a few additional species will be grouped at the end of this section on Sarcophagidae.

Dexosarcophaga Townsend

Four of eight species of Dexosarcophaga taken were either found over swarm raids of Eciton burchelli or were reared from the refuse deposits of this ant. It is noteworthy that the six specimens caught in a net (including three over swarm raids) were males, whereas 15 out of 30 adults reared from refuse deposits were females. Since no adults were taken near bivouacs or refuse deposits, it is possible that the females deposit eggs or larvae on or near the ants at the swarm front. The fact that all eight species are new strengthens the possibility that these species are associated with the army ants.

Records. The following specimens were taken on Barro Colorado Island except where another locality is given.

Dexosarcophaga currani Dodge. Over swarm raid of *E. burchelli*: 834 (1♂).

D. ecitocola Dodge. Over swarm raid of *E. burchelli*: 1782 (1♂); reared from refuse deposit of *E. burchelli*: 1841 (14♂, 14♀), refuse collected on 23 May with flies emerging on the following dates: 30 May (1♂), 2 June (2♀), 3 June (7♂, 9♀), and 6 June (6♂, 3♀).

D. halli Dodge. 30 March 1956 (1♂).

D. lopesi Dodge. 20 February 1956 (1♂).

D. nigricaudata Dodge. Over swarm raid of *E. burchelli*: 834 (1♂).

D. ravenna Dodge. PANAMA: Bejuco: 10 June 1956 (1♂) taken on flowering tree.

D. varia Dodge. Reared from refuse deposit of *E. burchelli*: 1550 (1♂, 1♀), refuse collected on 21 March 1956, adults emerged on following dates: 1 April (1♀), 2 April (1♂).

D. xon Dodge. 19 June 1956 (1♂).

Nephochaetopteryx

Approximately two thirds (44 out of 67) of the specimens of *Nephochaetopteryx* collected belong to five new species and were taken over swarm raids. Since more sweeping was done in the forest where no army ants were seen, it appears that these flies were attracted to the areas of the swarm raids. Unfortunately, the 41 females cannot be determined to species. Perhaps it is significant that the 26 males were all collected from February to April, whereas the females were taken from February to August. Nothing is known about the biology of any of these species.

Records. The following records from Barro Colorado Island are for males except for the first group of females determined only to genus.

Nephochaetopteryx spp. females. 27 January to 12 February 1955 (5), 12 to 13 February 1956 (2), 17 to 25 March 1956 (3), 26 May 1956 (1), 24 to 27 June 1956 (2), 29 July 1956 (1), 1 August 1956 (1); over swarm raids of E. burchelli: 834 (20), 1411 (1), 1415 (1), 1849 (2); over swarm raids of L. praedator: 1446 (1), 2257 (1).

N. aurescens Dodge. 13 February 1956 (1).

N. hyalina Dodge. Over swarm raid of E. burchelli: 1171 (1).

N. marianae Dodge. Over swarm raid of E. burchelli: 834 (5).

N. rettenmeyeri Dodge. 24 February 1955 (1), 20 to 29 March 1956 (5); over swarm raid of E. burchelli: 834 (10), over fan columns behind the raid swarm: 835, 12 February 1955 (1).

N. spinosa Dodge. 24 April 1956 (1); over swarm raid of E. burchelli: 834 (1).

Notochaeta Aldrich

Since more specimens of Notochaeta than of any other genus of sarcophagid were taken over the swarm raids, it is highly probable that at least some of the species have a biological connection with the raids. Seven new species and one previously described species were taken on Barro Colorado Island. Each of these species was found near army ants at least once, and less than three per cent of the specimens and only three species of Notochaeta were found where no army ants were present. One female was taken over a refuse deposit of E. burchelli, and several males and females were found within one meter of a bivouac of the same army ant. One male of N. amphibiae and two females of an undetermined species were taken from a group of flies hovering over or resting within a few centimeters of a black cricket covered with burchelli workers at the edge of a swarm raid.

On 15 March 1956 while watching a swarm raid of E. burchelli, I saw six or seven sarcophagids hovering over or resting on leaves in an area six centimeters square. There was a slight range in size, but all the flies looked like the same species. A single female of Notochaeta amphibiae (1447) was aspirated from the group. The leaves over which the flies were hovering were removed, and a frog 20 to 25 mm. long was found under them. At least two of the flies rested on the back of the frog, but no larvae were seen to be deposited. The frog showed no response to the flies and did not move when two burchelli workers ran over the frog but did not attack it. At the time when the frog was collected there was a small spot on the center of the back where larvae appeared to have been deposited, but no examination was made with a microscope. At 8:00 a.m. the following morning a small maggot could be seen moving in an open sore on the frog's back four millimeters behind the posterior margin of the right eye. By 8:00 p.m. that day the spiracular plates of nine maggots could be seen repeatedly pushing up to the surface of the hole. The hole at that time had been enlarged to about three millimeters in diameter and was slightly larger than the eye of the frog. At 8:30 p.m. the frog could still jump weakly, but within the next hour it appeared to get much weaker. The larvae and the hole in the back of the frog increased in size with the maggots constantly filling the opening with their spiracular plates. The following morning (17 March) at 7:00 a.m. the frog was dead, and the maggots were moving completely under the skin where they could not be seen. At 8:00 a.m. the next day the frog had been reduced to a skeleton within a small mass consisting mostly of skin. Nine larvae were crawling around inside the vial; and when dirt was added, they all crawled into it and pupated. The pupal period was 11 to 12 days with two females emerging on 29 March and six males emerging on 30 March (1447). The remaining pupa failed to develop.

Before the frog had been too severely damaged, it was compared with the reference collection of amphibians kept on Barro Colorado Island. The frog was determined as *Eleutherodactylus*, probably *E. diastema* (Cope) (Leptodactylidae). On the basis of the skeleton and skin the determination to genus was confirmed by Dr. Edward H. Taylor.

Although the above frog was not seen to be driven out from under leaves by the raiding army ants, other frogs have been seen jumping from the areas of raids. It appears that these flies may find hosts in a manner analogous to that used by *Calodexia* in locating its orthopteran hosts. Although Lopes (1946: 536-537) has reported that larvae from a female *N. aldrichi* Lopes developed in a oligochaete of the family Megascolocidae, no other possible hosts for *Notochaeta* are known to me. The larval period of 70 hours for *N. aldrichi* was about the same as that of *N. amphibiae*, and the pupal period of 13 to 15 days was two to three days longer. Lopes did not indicate whether oligochaetes are considered to be the normal host of *N. aldrichi*. He also reported that *N. confusa* larvae penetrated into an oligochaete but did not complete development.

Records for each species of *Notochaeta* taken on Barro Colorado Island are listed below with a summary given in table 7.

Notochaeta spp. females. Over swarm raids of *L. praedator*: 1277 (1), 1446 (1), 1575 (1), 1617 (2), 2202-J (1); over swarm raids or near *E. burchelli*: 834 (2), 991 (2), 1171 (1), 1172 (4), 1178 (3), 1412 (2), 1414 (3), 1415 (1), 1574 (4), 1756-A (1), 1756-B (1), 1757 (1), 1758 (6), 1782 (9), 1784 (4), 1790 (1), 1849 (4), 1854 (1), 2230 (4); over refuse deposit of E. burchelli: 890 (1).

N. amphibiae Dodge. Over swarm raids of L. praedator: 1575 (1♂), 1617 (1♂); over swarm raids of E. burchelli: 1411 (1♂), 1414 (1♂), 1447 (1♀), 1756 (1♂), 1782 (1♂), 1849 (1♂); over swarm of E. vagans: 2110 (2♂).

N. bisetosa Dodge. 13 February 1956 (1♀); over swarm raid of L. praedator: 1277 (1♂, 1♀), 1575 (1♀), 2206 (1♀); near bivouac or over swarm raids of E. burchelli: 991 (2♂), 1170 (1♀), 1414 (1♂), 1757 (1♂), 1860 (1♀).

N. frontalis Dodge. Over swarm raids of E. burchelli: 1170 (1♂), 1413 (1♂), 1755 (1♂).

N. fuscianalis (van der Wulp). 26 January 1955 (1♀), 15 to 19 February 1956 (2♀); over swarm raid of L. praedator: 1277 (1♂).

N. monochaeta Dodge. Over swarm raids of E. burchelli: 1849 (1♀), 1860 (1♀).

N. palpalis Dodge. 19 July 1956 (1♂); over swarm raids of L. praedator: 18 February 1955 (1♂), 1277 (1♂, 2♀), 1446 (2♀), 1617 (1♀), 2068 (1♀), 2178 (1♀), 2183-A (1♀), 2242 (3♀), 2257 (1♀); near E. burchelli: 991 (8♂), 1411 (1♂, 1♀), 1413 (1♂), 1414 (2♀), 1755 (2♀), 1782 (1♂), 2230 (1♂, 1♀), 2302 (2♀), 2329 (1♀), 2341 (1♀); over swarm of E. vagans: 2110 (9♂).

N. panamensis Dodge. Over swarm raid of L. praedator: 1575 (1♂).

Oxysarcodexia Townsend

At least nine species of Oxysarcodexia were taken on Barro Colorado Island, and six of these were found over swarm raids of E. burchelli or over a milling mass of E. vagans following the tearing apart of a bivouac. These species of sarcophagids are represented by single specimens except for one species also attracted to a dead armadillo. In addition, females of two species were taken in the laboratory, and nine adults were reared on beef from larvae squeezed from the abdomens of these two females. Although the above data indicate that species of Oxysarcodexia are not associated with the army ants or at least are not dependent upon these ants, there is a possibility that some of the species breed in the bivouacs or in the booty refuse outside of the bivouacs. One female Oxysarcodexia sp. was taken as it was larvipositing next to a bivouac of E. burchelli on 2 March 1955. This sarcophagid flew close to the bivouac and dropped one to three larvae in four to ten seconds and then flew off. A few minutes later the same fly, or one which could not be distinguished from it, returned and larviposited in the same general area. Although none of these larvae was reared, it should be mentioned that large cyclorrhaphous larvae, which may be Sarcophagidae, were found in refuse deposits and below another statary bivouac of E. burchelli. The above data suggest that several species of Oxysarcodexia may be associated with Ecitonini, but that their relationships with the ants are probably facultative. Since the specific determinations in some cases are still in doubt and additional data is so meager, no detailed records will be listed for Oxysarcodexia.

Other Genera of Sarcophagidae

The following species were also taken over army ants on Barro Colorado Island: *Anapunaphyto apicato* Dodge, *Duocheata veniseta* Dodge, *Panava inflata* Dodge, *Rettenmeyerina* sp., and another new genus and species. All except the last unnamed new genus are represented by only single specimens, and no observations were recorded on their behavior. However, 13 males of the last new genus were taken over *burchelli* swarm raids and over a milling group of *vagans*. Since this species was taken on four occasions and was never found where army ants were not present, its life cycle may be associated with the ants in some way. However, the fact that all specimens taken are males may indicate that this species was attracted only by the presence of the other flies.

Muscidae

Over 400 specimens of Muscidae (including Anthomyiidae) were taken on Barro Colorado Island during this project. About 25 species (determined by Fred M. Snyder) and somewhat more than half of the specimens are not considered to be associated with the army ants and will not be discussed. The only two specimens belonging to these species taken by sweeping over the swarm raids, belong to *Cyrtoneurina* Giglio-Tos, a genus known to live in dung and carcasses. Nine additional species of Muscidae show varying degrees of association with the Ecitonini. Three of these species breed in refuse from booty of *Eciton burchelli*, and these flies will be discussed under Arthropods Found in Refuse Deposits. The remaining six species are included below. Three reports of Muscidae associated with African Dorylinae are known to me, but I know of no reports of Muscidae with Neotropical dorylines. The African observations will be reviewed below under Comparisons Between Flies Associated with American and African Dorylines.

Polietina ecitonovora Snyder

Polietina ecitonovora is a new species whose biology is almost certain to be closely connected with the army ants since this fly was found so frequently over swarm raids. On only three of 24 occasions when the fly was taken, it was found where army ants were not raiding. *P. ecitonovora* was quite common over some swarm raids of *Eciton burchelli*, and on three days 24, 13 and 12 flies were taken over single swarm fronts. At one time four specimens were taken by sweeping the vegetation within one meter of a bivouac of *burchelli*. However, none was ever seen to lay an egg or to land near the bivouac or refuse deposits. In spite of the fact that more time was spent sweeping over swarm raids of *Eciton burchelli* than those of *Labidus praedator*, a disproportionate number of *P. ecitonovora* were taken over *burchelli*. Females outnumbered males over both species of ants by approximately three to one. The totals for the two ants are: *praedator*, 2♂, 9♀; *burchelli*, 23♂, 59♀.

Records. Barro Colorado Island, 15 February 1956 (1♀), 12 May 1956 (1♀), 7 July 1956 (1♀); over swarm raids of *L. praedator*: 1277 (2♀), 2155 (2♂, 1♀), 2178 (4♀), 2179 (2♀); within one meter of the bivouac or over swarm raids of *E. burchelli*: 827 (1♂), 834 (1♂, 23♀), 991 (2♂, 2♀), 1171 (1♂), 1178 (2♂, 2♀), 1412 (1♂), 1414 (1♀), 1415 (1♀), 1574 (1♀), 1755 (4♂, 8♀), 1757 (1♂), 1782 (5♂, 7♀), 1784 (1♀), 1790 (1♀), 1849 (2♂, 5♀), 1860 (1♂, 2♀), 2230 (2♂), 2258-X (1♀), 2329 (3♀), 2341 (1♀).

Other Species of Muscidae

The other species of Muscidae found over swarm raids of army ants are more doubtfully associated with the ants. Flies belonging to *Neodexiopsis* Malloch, *Neomuscina* Townsend and *Phaonia* Robineau-Desvoidy were taken near the ants, but these muscids were both less common over the ants and more common where the ants were not present compared with *Polietina ecitonovora*.

Neodexiopsis emmesa Malloch is represented in the collections by single females taken on three occasions over swarm raids. In addition, a single female belonging to a new species of *Neodexiopsis* was taken by sweeping in the forest where no army ants were present.

Records. Barro Colorado Island, over swarm raids of *L. praedator*: 1277 (1♀), 2179 (1♀); over swarm raid of *E. burchelli*: 1757 (1♀).

Three species of *Neomuscina* were taken over swarm raids of *E. burchelli* and *L. praedator*. Although there is no evidence at present that these flies breed in the refuse deposits of the army ants, it is possible that they do. The biology and taxonomy of the genus have been reviewed by Snyder (1949; 1954: 424-429) who reports that the species are saprophagous or coprophagous.

Records. The following specimens were taken on Barro Colorado Island.

Neomuscina conviva Snyder. 4 April 1956 (1♀); over swarm raids of *E. burchelli*: 2230 (1♂, 1♀), 2258-X (1♂), 2329 (2♂), 2341 (1♀).

Neomuscina nudinervis nudinervis (Stein). 4 to 7 August 1956 (3♂); over swarm raids of *L. praedator*: 2155 (1♀), 2201 (1♂); over swarm raid of *E. burchelli*: 1849 (1♂).

Neomuscina panama Snyder. Over swarm raid of *E. burchelli*: 1755 (1♀).

Phaonia cyrtoneuroides Snyder is a new species based on three specimens, two of which were taken over swarm raids of *L. praedator*.

Records. Barro Colorado Island. 9 May 1956 (1♀); over swarm raids of *L. praedator*: 1277 (1♀), 2178 (1♂).

Comparisons Between Flies Associated with American and African Dorylines

The African doryline ants of the genus *Dorylus*, commonly known as driver ants, also raid in large swarms and have many flies associated with their raids. No detailed study has ever been made of the behavior or biology of these flies, but there are scattered observations indicating that some of the flies are strikingly similar to, and others quite different from, those associated with Neotropical army ants. As mentioned above, *Stylogaster* is also found accompanying the raids of *Dorylus*, but there are apparently no reports of its attacking cockroaches. This genus is the only one found in common with the dorylines in both the Eastern and Western Hemispheres.

The conspicuous flies found with *Dorylus*, judging from the literature, all belong to the genus *Bengalia* Robineau-Desvoidy (including *Ochromyia* of authors). This genus of Calliphoridae is most unusual in that the adults are predaceous on a wide variety of insects. *Bengalia* apparently captures many insects in flight, but much of its prey is taken from *Dorylus* and other ants in raid columns. The most complete reports on this behavior are by Lamborn (1914a, 1914b, 1920), and his observations along with scattered reports by others have been reviewed by Bequaert (1922: 278-281). Although *Bengalia* usually has been reported as taking booty from the ants, it may also feed on the *Dorylus* brood, capturing larvae or pupae during emigrations. In addition, there is a report that the fly was seen to feed several times on the booty of an ant *without* carrying off the prey and *while* the ant remained holding the opposite end (Mellor, 1922). Like the flies with *Eciton*, *Bengalia* seems to find ant colonies by their odor. *Bengalia* is not known from the Western Hemisphere, and no flies with similar habits are known to be associated with Ecitonini. *Phaenicia purpurescens*, the common calliphorid found with swarm raids of Ecitonini, clearly could not have the same habits as *Bengalia* since the former genus has sponging mouthparts. *Bengalia* has a piercing proboscis "which is stiff and chitinized, with strongly toothed tip, directed forward" (Wheeler, 1928: 253).

Both the African and Neotropical Dorylinae have flies which oviposit at nest openings or next to the bivouacs. The most common African species is a calliphorid, *Tricyclea* van der Wulp (=*Zonochroa* Brauer and Bergenstamm), but at least one other calliphorid and an anthomyiid have similar habits (Lamborn, 1914b: vi-vii; Villeneuve, 1922: 522). It would seem more probable that these flies are breeding in the remains of booty captured by the driver ants rather than on the ants themselves. The muscids, *Neivamyia* sp., *Euryomma rettenmeyeri* and *E. panamensis*, and the sarcophagids, *Dexosarcophaga varia*, *D. ecitocola* and *Oxysarcodexia* sp., have been shown to breed in refuse deposits or next to bivouacs of *Eciton burchelli*. These will be discussed more fully under Arthropods found in Refuse Deposits. The muscid, *Stomoxys ochrosoma* Speiser, deposits eggs over raid columns, and these eggs may be carried back to the bivouacs of *Dorylus* (*Anomma*) *nigricans* Illiger (Thorpe, 1942: 38). *Neivamyia* sp. also deposits eggs which are carried both into the bivouac and to refuse deposits of *Eciton burchelli*.

Both the African and American dorylines have large numbers of Phoridae and a few Sphaeroceridae (Borboridae, Cypselidae) living in their colonies. In addition, a sciadocerid has been reported from *Labidus praedator* (Borgmeier, 1954: 297). These flies which are the only ones living as adults directly among the ants, will be discussed more fully below along with other myrmecophilous insects found within the bivouacs.

ARTHROPODS ASSOCIATED WITH NEOTROPICAL ARMY ANTS WITH A REVIEW OF THE BEHAVIOR OF THESE ANTS

(ARTHROPODA; FORMICIDAE: DORYLINAE)

VOLUME II

REFUSE DEPOSITS OF ARMY ANTS AND THE ARTHROPODS FOUND IN THEM

Descriptions of Refuse Deposits

Refuse Deposits of Eciton burchelli

All species of army ants apparently carry the remains of their prey, most dead workers, and empty cocoons to specific places called refuse deposits. Some refuse and most cocoons of the army ant broods are allowed to drop below the bivouac when the ants emigrate, and many dead workers are probably abandoned where they are killed in raids.

Species of army ants habitually capturing heavily sclerotized arthropods have larger refuse deposits than species primarily capturing immature insects. For this reason, Eciton burchelli (Westwood) has the largest refuse deposits of any species of army ant found in Panamá. Moreover, since epigaeic bivouacs and refuse deposits are more easily studied than hypogaeic ones, more information about them was obtained; this discussion is therefore primarily limited to the refuse deposits of burchelli with a few comparisons with those of other species.

After a sample of material from a refuse deposit of Eciton burchelli had been dried in a Berlese funnel to remove the living arthropods, the sample had a volume of 250 ml. and weighed 31 grams. Approximately 30,000 pieces of booty refuse were in this sample which contained little dirt or other extraneous material. The majority of the pieces were tarsomeres, tibiae, tentoria and phragmata which usually could not be determined to order. The predominating recognizable pieces were about 1,600 head capsules and other fragments of black ants. In addition to these, there were about 70 heads of burchelli workers. On the basis of observations of the refuse deposits in the field, dead burchelli workers had probably been placed intact on the refuse deposits, and staphylinids and other scavengers (discussed below) had dismembered the bodies. The other most common pieces which could be identified were head capsules and wings of Odonata, Orthoptera, Coleoptera and Hemiptera, pronota of cockroaches, and chelae and tail segments of scorpions. No vertebrate parts were found in any sample, although iridescent blue tails of lizards were seen being carried toward bivouacs on a few occasions. Parts of spiders consisted of an occasional chelicera, pedipalp, or leg segment; their scarcity (compared with captures seen during raids) indicates that burchelli can either eat or thoroughly tear apart the less heavily sclerotized exoskeletons of spiders. No traces of larval or pupal prey were found except for extremely rare pupal head capsules of ants killed shortly before emergence. It is not possible to get a total estimate of the booty by allowing the refuse to accumulate and then collecting it all after the colony emigrates. A large number of ants and other scavengers (discussed below under Arthropods Found in Refuse Deposits) are constantly carrying off the refuse even though most of it does not appear to have much food value. All the refuse around nomadic bivouacs of burchelli was usually eaten or removed within a few days after departure of the ants. Around statary bivouac sites the booty refuse also disappears rapidly, but the empty cocoons may be conspicuous for at least two weeks. The refuse deposits have a strong odor of rotting insects which is distinctly different from the odor of the ants themselves. Most of this smell probably comes from decomposing tissue within small pieces of booty like tarsomeres which the army ants do not cut open. When an army ant colony has young larvae, these penetrate within such small pieces of booty. However, no Eciton larvae were ever seen in refuse deposits. At the end of the nomadic phase and during the first one or two days of the statary phase the raids are usually the largest, and the lack of small larvae combined with the amount of booty collected probably account for a great amount of food remaining uneaten. Colonies at these times seem to have a stronger odor than those at the beginning of the nomadic phase.

Refuse deposits are located below the bottom edges of bivouacs with the exception of small deposits which sometimes are lateral to the bivouacs and on part of the bivouac supports. Thus, colonies bivouacked in brush heaps may have small amounts of refuse trapped on dead leaves or between junctions of fallen branches. In some locations it appeared that the refuse could have fallen or been dropped by the workers directly from the bivouac. Occasionally an ant drops an empty cocoon or some other object from the side of a bivouac. At other times empty cocoons, seen in the walls of bivouacs, dropped when the workers shifted their positions or emigrated. In contrast to empty cocoons which usually dropped from the bivouac, most of the booty refuse was carried out by workers. All workers seen carrying refuse were intermediates, never majors nor minors.

In laboratory nests, refuse of burchelli or other Ecitonini was usually scattered around the edges but was more concentrated in one or two corners when the workers were clustered in the center of the nest. The more refuse present in a nest the more it became generally distributed over the bottom.

It is not clear why the refuse is carried out of the bottom of the bivouac or is carried from other parts of the bivouac downward to refuse deposits. Probably most of the food is dropped many times by workers and larvae within the bivouac, and pieces which no longer have edible portions gradually fall to the bottom of the nest. By pushing aside lower portions of bivouacs, I have seen numerous pieces of booty in these areas and have seen a few pieces of refuse dropped directly under the bivouacs. Most raid columns enter the bottoms of bivouacs, especially when bivouacs are close to or resting on the ground; thus booty at least temporarily is more abundant near the bottom. Colonies which had raid columns entering the tops of bivouacs, nevertheless had refuse being carried out below. Even when refuse is allowed to fall directly under a bivouac, the workers do not let it accumulate there if the bottom of the bivouac is touching the ground or is a few centimeters from the surface on which the refuse lands.

At any hour of the day or night except during heavy rains one can find one to six short columns of ants extending for from two centimeters to two meters from the bottom of any bivouac. Even though no refuse was seen being carried along some columns, all these short columns from bivouacs will be called "refuse columns". Such columns were not for raiding although on a few occasions raid columns were developed along the same routes. The traffic on these short columns seldom exceeded a single ant in width, and usually the columns had workers spaced every two to six centimeters. Regardless of the amount of traffic on these columns, most of the workers were not carrying anything. At times workers carried the same piece of booty refuse or part of an empty cocoon, especially a cocoon from a male or queen of burchelli, back and forth along the refuse columns for more than one hour. Workers of burchelli were not seen to feed in the refuse deposits or along the columns to them except when the workers were eating male or queen pupae from their own colony.

Since workers defecate while running along the refuse columns, these columns may be an adaptation for helping to keep the bivouacs clean. Nothing is known about the extent of defecation within the bivouac or along raid and emigration columns except that fecal spots are much more infrequent along these trails than along refuse columns in proportion to the number of workers using them. In addition, white spots of fecal material were most noticeable along refuse columns during the statary phase when raiding decreased; and during one statary phase the spots appeared to increase most rapidly on days when raiding was absent or minimal. In some places the spots of fecal material formed a solid trail about one centimeter wide. These spots are not the chemical trail which the army ants follow along columns, and there was no indication that the workers were attracted to the fecal material of workers as they were to the fecal material of the queen.

Figures 65 to 68 are diagrams of typical refuse columns and deposits of burchelli. In all cases the refuse deposits were at least 20 cm. away from the edge of a bivouac although scattered pieces of refuse could be found closer. In figure 68 the refuse deposit appears to extend to the base of the bivouac, but actually the bottom edge of this colony, clustered on the side of a tree, was about 20 cm. from the refuse. The maximum distance from the bivouac is usually one meter, but a few refuse deposits were found farther away when refuse columns extended down steep slopes. For example, a colony bivouacked on a bank had one refuse deposit two meters down a slope of 80°. The longest refuse column seen extended from a statary bivouac near the crown of a tree to a large refuse deposit between buttresses at the base. Much of the refuse was carried by workers more than ten meters down the trunk of the tree.

However, some of the refuse was seen being dropped by workers which came down to within one or two meters of the ground; and judging from the wide dispersion of the refuse, much of it had been dropped from higher up the tree or from the bivouac itself. Five other colonies which had statary bivouacs high up in trees did not have refuse deposits at the ground level. Some pieces of refuse and empty cocoons were seen on the ground, and it is possible that in these five cases all the material was dropped from near the bottom of the bivouac or most of it stayed in the cavities where the bivouacs were located.

The ants move along lines of least resistance and will follow grooves or run along the edges of logs, lianas or roots. A good example is shown in the upper part of fig. 66 where an especially heavy concentration of refuse was dropped in the depression and crack next to the edge of a buttress root. In a similar manner when burchelli is bivouacked between the buttresses of a tree, the workers often deposit refuse along the edges of the buttresses even when there is level ground sloping away from the bivouac (as in fig. 68). If small depressions were made near a bivouac, especially along the refuse columns, the workers at times used these depressions for refuse deposits.

Outside of such physical factors, there was no obvious reason why the ants deposit refuse in one area and not in others. Nomadic colonies which stayed in the same site for only one or two nights had fewer and smaller refuse deposits than statary colonies. (Compare figs. 65 and 68 with figs. 66 and 67 for statary colonies.) Statary colonies were seen which had over 20 refuse deposits, and the constant shifting or activity from one to the other of these from day to day often obscured the boundaries between adjacent deposits. The refuse deposits of colony '55 B-IV during its statary period of 21 days (12 February to 3 March 1955) are diagrammed in fig. 66. Since colonies of burchelli probably are seldom larger than this one, it should have had about the maximum amount of booty refuse and dead workers. Colony '55 B-IV also had a brood of reproductives in cocoons, and this may have increased the size and number of raids during that statary phase. The raids of this colony seen on the final three days of the preceding nomadic phase were maximal in size. There were no peripheral connecting columns between any of the refuse columns except for the trail ne curving to refuse deposits ne and el. Even where refuse deposits were separated by only two centimeters of level ground, such as ne and el, workers rarely went from one to the other but would constantly go to and from the bivouac.

The number of refuse deposits around any one bivouac appears to be primarily dependent upon the length of time the colony stays in the site and the slope and type of surface within a meter of the bivouac. When a colony bivouacked within a hollow tree with a single large depression near ground level inside the hollow trunk, the entire refuse was found in this single depression. Refuse was divided into several deposits when the bases of similar trees had a number of small depressions in them. Statary bivouacs which were largely within hollow trees, but with part of the colony exposed, deposited most of the refuse outside of the cavity. An example in which all the refuse was carried away from the tree is shown in fig. 67.

The most detailed records of the activity in refuse columns and the amount of refuse deposited were taken for colony '55 B-IV. This colony was visited almost every day during its statary phase, and for the last 15 days of the phase the colony was usually visited two to four times a day and often was watched for several hours each day. The following tentative generalizations regarding activity along refuse columns and in refuse deposits are based primarily on observations of this colony supplemented by records from about 25 other colonies. All statements refer to both nomadic and statary colonies unless one phase is specified.

(1) At least one refuse column is usually present any time during the day or night, but the column may shift its position slightly or be abandoned as a different column is started. (2) When several columns are in use, the traffic on the columns may or may not increase or decrease simultaneously. (3) The activity on refuse columns usually increases during the day and is minimal during the night when all workers are in the bivouac. (4) Refuse columns can start after 8:00 p.m. and stop before 8:00 a.m. the following morning. (5) The amount of ant traffic on a refuse column at any one time is not a reliable indicator of the amount of refuse being carried along that column. (The total traffic throughout a 24 hour period probably would give an accurate estimate.) (6) A colony may use one refuse deposit extensively for several days and then shift to another deposit closer to or farther from the bivouac but along the same refuse column. One column may be used extensively, then be abandoned for a few days, and then be used extensively again. (7) Refuse occasionally is carried by workers from the refuse deposits back to the bivouac. (8) Sunlight striking a bivouac when no raid is in progress will increase the traffic on all refuse columns but especially on those near the side of the bivouac away from the sun. (9) The start of a raid will usually decrease the amount of traffic on refuse columns near the raid column. (10) The amount of activity on the refuse columns often increases just before a raid starts. (11) Most inedible parts of booty

are put in refuse deposits within 24 hours of the time of capture. (12) Even though many pieces of booty are divided into several pieces of booty refuse, the number of pieces of refuse found in the deposits must be less than ten per cent of the number of pieces of booty collected. (13) The maximum amount of refuse added to the deposits in one day is about 100 ml.

Refuse Deposits of Other Species of Army Ants

Since *Eciton hamatum* has epigaeic bivouacs similar to those of *burchelli*, one might expect the refuse deposits to be approximately the same. However, the smaller size of *hamatum* colonies and the fact that this species seldom captures heavily sclerotized prey are responsible for a much smaller amount of refuse. Refuse columns seldom exceeded 30 cm. in length and distinct refuse deposits were almost impossible to find even for statary colonies (not including the empty cocoons from the brood). Statary colonies may have a slightly stronger odor than nomadic colonies due to accumulated refuse, but colonies at the end of the statary phase have a much weaker odor than the refuse from nomadic colonies of *burchelli* after a single day. In the period of two hours only two or three workers were usually seen slowly walking along what might be refuse columns at the base of a bivouac. These workers were so infrequent that it was not practical to determine whether they followed regular refuse columns or how much refuse was carried. The position of scattered booty refuse indicated that it must have been carried out by the workers. Scavengers were much less frequent than with *burchelli* colonies, but some booty remains were carried away from refuse deposits of *hamatum* colonies. It is possible that part of the booty refuse seen

20 to 30 cm. from *hamatum* bivouacs could have been carried part of that distance by the scavengers. However, the army ant workers were also seen to go out that distance.

Since *Labidus praedator* captures large numbers of sclerotized arthropods as does *burchelli*, it probably has refuse deposits which are fairly large. However, its bivouacs are subterranean, and most refuse is apparently deposited in widely dispersed cavities around the nest. When the workers were seen coming out of the ground at holes thought to be over the bivouac, an occasional piece of booty remains was carried out and dropped near these holes. Other subterranean species, such as *E. dulcius* and *vagans*, also carry small amounts of booty refuse out of their bivouacs and deposit the pieces of arthropods along with dirt carried out of the nest. These cases are the only ones seen in which the refuse was carried higher than the level of the bivouac. No dead workers of any species except *hamatum* and *burchelli* were ever seen being carried out of bivouacs or lying among booty refuse.

Arthropods Found in Refuse Deposits

The arthropods found in refuse deposits were studied using three main techniques: (1) observations on refuse deposits in the field and on samples from these deposits kept in dishes in the laboratory, (2) rearing of adult flies from samples of refuse kept in jars in the laboratory, and (3) extraction of living arthropods by means of a Berlese funnel. Although some arthropods were aspirated from the refuse, the majority were extracted by Berlese funnels immediately after the samples were collected. A set of ten funnels, each 20 cm. in diameter, was used; and a typical sample would fill one funnel. Large samples from an entire statary phase would require three to ten funnels. Berlese samples for comparison were also taken of soil immediately below the bivouacs, soil below the refuse deposits at depths of one to two centimeters and two to five centimeters, and leaf litter and soil in comparable areas within logs and on the forest floor where neither bivouacs nor refuse deposits were present.

It will take at least several more years before most of the species thought to be associated with the ants or the refuse deposit can be identified or described. Consequently most of the arthropods are included below under family names or other higher categories. The samples were not weighed or measured, and none has been sorted completely to family level. No attempt has been made to analyze the samples quantitatively except for subjective judgments as to which groups are considered abundant, common, or rare. Over 100,000 arthropods are included in the 115 samples taken from refuse deposits and under bivouacs. Consequently, a more complete sorting was not feasible, and I looked primarily for arthropods suspected of being associated with the ants.

Ricinulei

One species of Ricinulei, *Cryptocellus centralis* Fage, was reported from a nest of *E. hamatum*; however, it was questioned whether the species is normally found within ant nests or may have been in debris bordering the nest (Fage, 1938: 370-371). No specimens of ricinuleids were taken in Panamá during this study, and the above species is probably not a myrmecophile.

Chelonethida

Pseudoscorpions, found in nests of many kinds of ants (Donisthorpe, 1927: 182-183), probably feed on microarthropods rather than the ants. One specimen was aspirated along with workers of *Labidus praedator* from a raid column, but it probably was booty of the ants. A second specimen, taken with a sample of *E. burchelli* from a bivouac, also was probably booty. Pseudoscorpions were found in small numbers in many of the refuse deposits where they were apparently attracted by the abundance of food. Although over 20 pseudoscorpions were found in refuse deposits of a single colony, equally large numbers were found in other areas, such as moist rotting wood containing abundant microarthropods. Perhaps because the refuse deposits of *burchelli* are smaller and less permanent, they have fewer pseudoscorpions than those of *Atta cephalotes*. No pseudoscorpion was found riding on an ant.

Phalangida

One species of phalangid, Neopucrolia borgmeieri Mello-Leitão, was found within the subterranean nest chambers of E. dulcius dulcius in Argentina (Bruch, 1923: 217-218). Later Bruch (1929: 437) stated that it was not considered a true guest. No phalangids were taken within bivouacs on Barro Colorado Island, but on two occasions individuals were seen feeding on the remains of booty in refuse deposits of burchelli. The phalangids apparently visit the refuse deposits for feeding without staying in them for a long time.

Araneida

Although at least seven species of spiders have been reported to be found with Ecitonini, there is no evidence that any of them are primarily restricted to refuse deposits, but one or two species have been considered to be true myrmecophiles (Fage, 1938: 369-375; Mello-Leitão, 1925: 237; 1926: 2; Bruch, 1929: 437). On Barro Colorado Island spiders were relatively rare in refuse deposits, and most specimens found were small and immature. Salticidae were common on the forest floor, and they were seen visiting the refuse deposits and feeding on the scavenging nondoryline ants as well as the live army ants in the refuse columns.

Acarina

The mites were the most abundant order of arthropods both in number of species and number of individuals found in all samples from refuse deposits. Although many species of mites are found on the army ants, these species were never or rarely found in the refuse deposits. The absence of these mites is attributed to the fact that when a worker dies, mites leave it and get on living workers. In addition, most of the mites are too small to be carried by the workers, and when the mites die, they probably fall below the bivouac or along columns. A few Circocyllibanidae and Planodiscidae were found in refuse deposits. No immature stages suspected of belonging to any of the myrmecophilous or ectoparasitic species of mites were found in the refuse deposits. It is possible that some of the Uropodidae that are phoretic on the army ants breed in the refuse, but these mites were rarely found on the adult ants or within bivouac samples. Anoetid and acarid hypopi were common both on the workers and in the booty refuse. Perhaps the life cycle of some of these species is partially in the refuse deposits. Adults of these two families (but possibly other species) were found feeding in refuse deposits, but it is not known whether the hypopi were getting on or leaving the workers there. The species of Neoparasitidae (?) tentatively called "species A-1" was the only mite frequently found in refuse deposits of _E_. _burchelli_ and also known to be parasitic on the adult and larval ants. Deutonymphs of two species of Parasitidae were found attached to wingless female Phoridae taken in refuse deposits. The life cycle of neither the mites nor the phorids is known, but both may breed in the refuse since they were common there.

In addition to the above mites, the following families were represented in the samples from refuse deposits: Liroaspidae, Parasitidae (common), Veigaiaidae, Macrochelidae (abundant), Neoparasitidae (common), Laelaptidae (abundant), Phytoseiidae (common), Rhodacaridae (abundant), Uropodidae (abundant), Prodinychidae, Phaulodinychidae, Urodinychidae, Trachytidae, Polyaspidae (common), Scutacaridae, Pyemotidae, Tydeidae, Ereynetidae (abundant), Cunaxidae (common) Bdellidae, Labidostommidae, Trombiculidae (common), Acaridae (abundant), Glycyphagidae, Saproglyphidae, Anoetidae (mostly hypopi, abundant), Hermanniidae, Neoliodidae, Hermanniellidae, Lohmaniidae (common), Hypochthoniidae (common), Eremaeidae, Belbidae, and Phthiracaridae. In addition to the above list, there must be at least ten other families in the material collected. However, there is no evidence that most of the species of the above families are really associated with the ants, and it is thought that they are concentrated in refuse deposits because of the abundant supply of food there compared with adjacent areas of forest floor.

Diplopoda

Myrmecophilous millipeds were found on Barro Colorado Island in columns of Labidus and Nomamyrmex, but the diplopods found in refuse deposits of E. burchelli were never seen to follow any of the ant columns. Since the species found in the refuse deposits were either rare or were found as frequently in areas of litter, they are assumed not to be myrmecophiles.

Thysanura

The three species of Thysanura found with army ants on Barro Colorado Island appear to be panamyrmecophilous. Although one might expect that these species might move from one colony to another and be scavengers on booty refuse, no specimens were found in the refuse deposits.

Collembola

In the refuse deposits the Collembola are second, following the mites, in number of species and specimens. Most of these belong to nonmyrmecophilous genera known from leaf litter and include the following genera or species (determined by Dr. F. Bonet): *Willemia persimilis* Bonet, *Proisotoma* n. sp., *Folsomina onychiurina* Denis, *Isotomina thermophila* Denis, *Entomobrya simulans* Denis, *Pseudosinella wahlgreni* (Börner), and *Pseudosinella argentea* Folsom. In addition to the above Collembola, a few specimens of two species of *Cyphoderus* were found in refuse deposits of *E. burchelli* and *hamatum*. These species are probably myrmecophilous like a number of other Cyphoderidae. Other definitely myrmecophilous springtails were not found in refuse deposits although at times they were numerous in bivouac samples or ant columns. Unfortunately, less than one third of over 500 specimens of Collembola taken associated with army ants have been determined, and additional conclusions should be postponed until all the determinations are completed.

Hemiptera

On several occasions Reduviidae were found eating worker army ants along refuse columns and in refuse deposits, as well as along raid columns. These predators were females and nymphs of *Apiomerus* and *Opisthacidius* ? (or *Zelurus* ?) (determined by P. Wygodzinsky). There is no evidence that either one is attracted to the refuse deposits. Apparently these bugs wander around on tree trunks and the forest floor and capture insects of various kinds wherever they can. *Apiomerus* sp. was also found eating males of *Neivamyrmex* or *Eciton* on two occasions at a light. Opisthacidius sp. is an inconspicuous bug covered with dirt which may be an important protective adaptation since E. burchelli workers were seen to run over the bug without attacking it. Since Opisthacidius apparently frequents areas of dirt and dry rotting wood which match the particles found on all the specimens, these bugs would be found in typical bivouac sites of burchelli.

Lepidoptera

A small number of minute caterpillars were found in Berlese samples from refuse deposits, and five adult microlepidoptera were reared from booty refuse. It has not yet been possible to get these determined, and nothing is known about their life cycles.

Diptera

The Diptera and Coleoptera are the two most important groups of insects found in the refuse deposits as well as within the bivouacs. In both orders some species are frequently found both in the refuse deposits and along the ant columns and other species are restricted to the refuse deposits. The latter species will be considered here, and those found more frequently along with the ants will be discussed below in the sections on myrmecophiles in columns and bivouacs.

The most important families of Diptera associated with refuse deposits are Phoridae and Muscidae. In addition, there are some Sphaeroceridae (=Borboridae and Cypselidae) which appear to be associated with the army ants. Larvae of sphaerocerids are known to be scavengers in a wide variety of nests of mammals and insects including ants (Richards, 1930: 319-323). Species have been described from nests of Anomma in

Africa (Richards, 1950, 1951), and at least two species, *Aptilotella borgmeieri* Duda (1924) and *Homalomitra ecitonis* Borgmeier (1931) have been described from *Eciton s. lat.* and *L. praedator*. A few specimens of several species were found in Berlese samples from refuse deposits of *burchelli*, but none of these flies has been determined.

Phoridae: About 34 species of Phoridae were taken on Barro Colorado Island in association with Ecitonini, and 19 of these species were found in refuse deposits. *Thalloptera schwarzmaieri* Borgmeier is the only one of the 19 species not found with *E. burchelli*, and this phorid is clearly a myrmecophile since it was found running in the columns of the army ants at least ten times. It was found in the refuse of one colony of *hamatum* at the same time that it was running back and forth along refuse and raid columns. Eleven of the remaining 18 species were never found running in columns or within samples of ants from bivouacs. These 11 species were found only in refuse deposits of *burchelli*, except for *Apterophora attaphila* found also in refuse of *hamatum*. As indicated by the name, this species is known from *Atta*, and probably it is found in refuse of a number of different ants. Perhaps none of these 11 species is a myrmecophile in a strict sense, because all were found solely in the booty refuse. However, *Ecitoptera concomitans* was found in a column(s) of *E. dulcius dulcius* in Argentina and is considered a true guest (Borgmeier and Schmitz, 1923: 212-215; Bruch, 1929: 436). Three of the species were also found in samples of detritus from the forest floor where no army ants were present. The seven remaining species which were found in refuse deposits and in bivouac samples or running along columns were not found in samples of detritus where there were no army ants. One possible exception is *Puliciphora boringuenensis* Wheeler which was reared from the remains of dead insects (including army ants) in a laboratory nest of *burchelli*. A single specimen was found in a sample of *Nomamyrmex esenbecki* aspirated from a raid column. However, this phorid was not seen running in the column, and it may have been picked up from the dirt. One specimen was found on decaying beef, and two specimens were reared from a cockroach taken as it was escaping a swarm raid of *L. praedator*. It is more likely that the eggs or larvae from which these two phorids developed were deposited on the cockroach after it died rather than at the time it was escaping the swarm raid. (The two adult phorids were found in the vial with the dead cockroach 11 days after the cockroach was taken, and about 25 larvae were found two days later. These larvae are thought to have developed from eggs laid by the two adult phorids which probably got into the vial through the cloth cover.)

The following alphabetical list of Phoridae includes those species taken during this study at least once in refuse deposits or in detritus under or around bivouacs of Ecitonini. Species taken only in columns or bivouac samples are not included here except for those names preceded by asterisks which indicate species also found within refuse deposits. The species of ants with which the flies were associated and the habitats where the flies were found without army ants are also listed. More detailed records will be given in the later section on Phoridae found within bivouacs.

Apterophora attophila Borgmeier (6♀): *E. hamatum*, *burchelli*.

Chonocephalus buccatus Malloch (8♀): *E. burchelli*; rotten wood and detritus in hole in fallen tree.

**Diocophora appretiata* Schmitz (1♂, 1♀): *E. burchelli*.

*_Dohrniphora ecitophila_ Borgmeier (4♀): _E. burchelli_, _dulcius_.

Dohrniphora paraquayana Brues (2♀): _E. burchelli_.

*_Ecitophora bruchi_ Schmitz (17♂, 14♀): _E. burchelli_, _vagans_, _mexicanum_.

*_Ecitophora collegiana_ Borgmeier (42♀): _E. hamatum_, _burchelli_, _vagans_, _dulcius_, _mexicanum_.

Ecitoptera centralis Borgmeier (1♂, 1♀): _E. burchelli_.

Ecitoptera concomitans Borgmeier and Schmitz (2♀): _E. burchelli_.

*_Ecituncula_ (_Labidoncula_) _halterata_ Borgmeier (467♀): _E. burchelli_, _vagans_, _L. praedator_, _Noma. esenbecki_.

*_Ecituncula tarsalis_ Borgmeier (642♀): _E. hamatum_, _burchelli_, (?) _L. praedator_.

Homalophora epichaeta Borgmeier (8♀): _E. burchelli_.

Pulicimyia triangularis Borgmeier (77♀): _E. burchelli_; leaves and dirt from forest floor.

*_Puliciphora borinquenensis_ Wheeler (10♀ and 93 [sex?] reared in laboratory): _E. burchelli_, (?) _Noma. esenbecki_; leaves and dirt from forest floor; emerged from dead cockroach; found on decaying beef.

Puliciphora fenestrata Borgmeier (17♀): _E. burchelli_.

Puliciphora frivola Borgmeier (5♀): _E. burchelli_.

Puliciphora imbecilla Borgmeier (13♀): _E. burchelli_.

Puliciphora rata Borgmeier (2♀): _E. burchelli_; dirt and detritus from forest floor.

*_Thalloptera schwarzmaieri_ Borgmeier (300♀): _E. hamatum_, _vagans_, _dulcius_, _mexicanum_, _L. praedator_.

Sarcophagidae: Two species of Sarcophagidae were reared from booty refuse, and a third species was taken as it was flying around the refuse deposits. At different times other flies which were probably Sarcophagidae were seen visiting refuse deposits, but none of these flies were caught. Numerous fly larvae taken in refuse deposits also indicate that probably several more species of sarcophagids breed there.

Notochaeta sp. One female flying over a refuse deposit and two flying near a bivouac of *E. burchelli* were taken; but since 58 other specimens were caught over swarm raids, this genus may not breed on the booty refuse. However, for all species of *Notochaeta* taken on Barro Colorado Island, only five specimens were taken by sweeping where army ants were not present compared with 133 taken near army ants.

Dexosarcophaga varia Dodge. One male and one female were reared from booty refuse taken at a bivouac site used by a colony of *E. burchelli* on the fourth day in a nomadic phase. The booty refuse was collected on 21 March, the fifth nomadic day. The female and male emerged on 1 April and 2 April, indicating a developmental time from larva to adult of 11 to 12 days. No other specimens were taken.

Dexosarcophaga ecitocola Dodge. One male of *D. ecitocola* was taken over a swarm raid of *E. burchelli*, and 14 males and 14 females were reared from a sample taken from a refuse deposit of *E. burchelli* used during a statary phase. Since the larvae may have been deposited at any time during the statary phase, it is impossible to determine the length of the developmental period.

Muscidae: Three species of Muscidae were reared from booty refuse of *E. burchelli*. There is the possibility that other species of Sarcophagidae and Muscidae (including Anthomyiidae) may have similar habits, but the other flies seen near bivouacs and in refuse deposits were much more rare and were not caught.

Euryomma Stein. *Euryomma panamensis* and *E. rettenmeyeri*, both described by Chillcott (1958), were taken in and around the refuse deposits of *E. burchelli*. No other specimens of *Euryomma* were taken except for one male of *panamensis* taken over a swarm raid of *burchelli*. Both species were present in or around the same refuse deposit, but *E. panamensis* was somewhat less common than *rettenmeyeri*. Presumably the species have similar behavior; however, the species were not distinguished in the field. Mating pairs were observed several times, but males were much more common than females at refuse deposits. One reared series included 23 males and 24 females indicating that males and females are produced in approximately equal numbers. All immature stages of both species, except for the egg and puparium of *panamensis*, were described by Chillcott (1958) from specimens taken in refuse of *Eciton burchelli*. These are the first immature stages known for the genus, but related genera such as *Fannia* breed in excrement and decaying organic material. The larvae were abundant where there was a large amount of booty refuse, and one exceptional sample contained 439 larvae of *Euryomma* in addition to 435 other dipterous larvae. Perhaps these two species of *Euryomma* are restricted to refuse deposits for breeding sites, since those flies were found at almost every refuse deposit where a search was made. They were not found near dead mammals, rotting fruit or vegetation, or excrement. When several refuse deposits were present around the same bivouac, *Euryomma* was most abundant around the one with the most recent refuse. Both males and females found the refuse columns of nomadic colonies before 7:00 a.m. when there was little or no refuse near the bivouac on the morning following an emigration. Because one specimen was also taken over a swarm raid, *Euryomma* probably is attracted by the odor of *burchelli* as well as by the odor of the refuse deposits themselves. *Euryomma* was never found near any other species of army ant.

Euryomma frequently runs about on the surface of the refuse and flies five to ten centimeters away if an ant touches it. Although the ants sometimes darted at the flies, no *Euryomma* was seen caught. Rarely *Euryomma* would fly toward the bivouac, but adults did not stay there and never ran in columns with the ants. The adults were seen all day long and were even active in the evening when it was too dark to see them without a flashlight.

Records. Detailed collection records for the above two species of *Euryomma* were published by Chillcott (1958).

Neivamyia sp. A new species of *Neivamyia* Pinto and da Fonseca (determined by Fred M. Snyder) was also reared from refuse deposits of *E. burchelli*. However, the behavior of the adult flies is markedly different from that of *Euryomma*. *Neivamyia* never rests on any surface near a refuse deposit or bivouac. Males were never taken near bivouacs; but if we were not too active around colonies, at least several females could usually be seen within an hour during the day at any bivouac of *burchelli*. One male and one female were taken on Barro Colorado Island where no army ants were seen. The females were readily recognized by their manner of hovering and by their shiny grayish-blue abdomens. They are alert flies, flying away if disturbed, but usually the same or a different individual came to the bivouac within a few minutes. The maximum number of flies seen at one time was 12. Twenty flies were collected in about a half hour on two occasions without noticeably decreasing the number visiting a bivouac. The females flew up to the edge of a bivouac and hovered usually only one to three and never more than five centimeters from the wall of ants. By moving up to them slowly, I could aspirate the flies. If there was a hole in the side of a bivouac due to an exodus of ants on a raid column, Neivamyia even flew into the hole. With little movement of its body each fly laid an egg every one to ten seconds while hovering in one spot. All flies seen at bivouacs were ovipositing. Sometimes the eggs were deposited so rapidly that a second egg would stick to the preceding one, and the two would fall together. Most eggs were dropped close to the bivouac, but at times the flies oviposited while flying slowly out along a refuse column. They usually flew at a height of about two centimeters but sometimes dropped to less than one or went as high as eight centimeters above the column. More eggs were layed over refuse deposits than over refuse columns, and only one was seen dropped outside of these areas. A fly occasionally flew a few centimeters along a raid column, but Neivamyia was clearly more frequent over refuse columns. On one occasion a fly was seen flying over a spinning cluster, but no eggs were laid there. Apparently Neivamyia is attracted primarily by the odor of the refuse.

When the flies were hovering next to the face of a bivouac, they most frequently were less than 20 cm. from the bottom edge of a bivouac touching the ground; and when a bivouac extended higher than 50 cm. above the ground, the flies seldom flew above that level. The highest point at which eggs were laid was 80 cm. above the ground (and base of the bivouac). No Neivamyia was seen near bivouacs which were not close to the ground.

Neivamyia was seen ovipositing as early as 6:43 a.m. when the sunlight was only striking the upper parts of trees, and the females remained active after 7:00 p.m. when flashlights were needed to watch them ovipositing. It appeared that the flies oviposited more during late afternoon and early evening, but they were seen ovipositing at all hours of daylight.

The eggs are 1.4 to 1.6 mm. in length and pale brownish-yellow, close to white. They were easy to see on the ground and while they were being laid. Single flies were seen to lay up to 32 eggs which probably is close to the maximum ready to be laid at one time. The large number of eggs produced at one time suggests that the females may die after they lay a single batch of eggs. Small intermediate workers carried the eggs and first instar larvae into the bivouac or to refuse deposits. When these workers were picked up with forceps by the alitrunk or gaster, they dropped the apparently uninjured eggs or larvae. Some eggs laid by a female put in a laboratory nest (ca. 20 cm. x 20 cm. x 2.5 cm. high) were picked up by workers, mouthed for as much as ten minutes, and placed in a refuse deposit in a corner of the nest. The adult fly was finally killed by the ants, but except for one leg and parts of the others, the fly was not torn apart nor eaten. None of the eggs was noticeably injured, but some may have been killed by being pinched by the mandibles of the workers. Some eggs hatched between 24 and 48 hours after laying, but attempts to rear isolated larvae on dead insects were unsuccessful. However, a total of 67 males and females were reared from samples of booty refuse kept in jars in the laboratory. A total of 33 adults was the largest number reared from booty refuse placed by a nomadic colony in a single refuse deposit. In the field fewer probably would have survived primarily because of attacks by staphylinid larvae and adults (most of which had been removed from that sample). About 90% of these Neivamyia emerged on the ninth or tenth day after the eggs were laid, and the remaining emerged on the 11th or 12th day.

It is not clear whether the eggs or larvae picked up by the army ants and carried into bivouacs survive or whether they are eaten. Perhaps only those survive which are laid directly in the refuse deposits or placed in them by the workers. Since some refuse deposits are in hidden cracks to which it would be difficult or impossible for *Neivamyia* to fly, having its eggs carried to the refuse deposits by the army ants is a distinct advantage for the survival of this fly.

Thorpe (1942) reported that one specimen of *Stomoxys* *ochrosoma* Speiser laid one egg over a column of *Dorylus* (*Anomma*) *nigricans* in Tanganyika. The female hovered about one inch over the ants which were returning to the nest with booty. "The fly held or steadied the object [presumably an egg] with its legs for a few seconds and then dropped it into the column, apparently aiming it with great care and precision exactly in front of one of the rapidly marching workers which happened to be returning without booty. Without a moment's hesitation, ...the worker picked up the white object...and continuing its homeward march disappeared from view a few inches farther on...." No additional specimens of the fly could be found over the doryline columns. The adults are known to suck blood from mammals like other species of *Stomoxys*, and Thorpe speculates that the larvae are scavengers in the bivouacs of the driver ants and do not feed on the ants themselves.

In comparison, the females of *Neivamyia* sp. do not "aim" their eggs at "empty-handed" workers but deposit them over columns regardless of whether workers are directly beneath. The females also do not hold eggs with their legs as *Stomoxys* was seen to do. I know of no further observations on the behavior of *S.* *ochrosoma*, but Thorpe (1942: 39) stated that it was reported from over army ants on two other occasions.

Records. Several hundred females were seen ovipositing next to bivouacs of E. burchelli on Barro Colorado Island. A sample of 25 specimens was taken on 22 February 1955, 19 and 23 February 1956. A total of 67 males and females was reared from booty refuse taken from five bivouac sites between 21 and 28 March 1956. In addition, one female was taken on 28 May 1956 and one male on 16 June 1956. Although the above records of Neivamyia associated with burchelli are from February and March, the flies were seen ovipositing from February through August 1956 with no seasonal changes observed.

Coleoptera

More Coleoptera were found than any other order of insects in the refuse deposits of Eciton burchelli. The majority of specimens of both adults and larvae belong to the family Staphylinidae, but more than 20 families of beetles are represented in this habitat. The families found most frequently or known to include myrmecophilous species are discussed separately below. In addition, the following families were represented: Scaphidiidae, Scydmaenidae (abundant), Dermestidae, Nitidulidae (Omosita?, common), Cisidae, Phalacridae (Phalacrus, abundant), Ptiliidae (Micridium, etc., common), Diphyliidae (Diplocoelus), Scolytidae, and Aphodiidae (Ataenius). I am indebted to Dr. Wilbur R. Enns for identifying most of the beetles in the above list. There is no indication that any of these beetles are myrmecophiles, and many of them may have been present by chance. The Scolytidae and Ptiliidae appeared to have been most abundant in samples including rotten wood and probably were in the habitat before the army ants bivouacked there. Others such as the Scydmaenidae and Phalacridae, judging from their abundance, most probably were not in the area of the bivouac before the ants arrived but were attracted to the refuse deposits. Since *E. burchelli* has difficulty capturing small hard-bodied insects, the small size of almost all of the above beetles may be an important adaptation for their survival.

Limulodidae: Limulodidae are clearly among the true myrmecophiles within colonies of Ecitonini, but no specimens were ever seen in refuse deposits. However, in Berlese samples of booty refuse eight specimens were found. In spite of the small size of these beetles, the small number of specimens found within the booty refuse could not be attributed to overlooking the limulodids since about 1,130 specimens were found associated with the army ants.

Staphylinidae: Over 7,000 Staphylinidae were collected from refuse deposits of *E. burchelli* on Barro Colorado Island, and many thousands more could have been collected had there been any prospect of getting the specimens determined. I am indebted to Dr. Charles H. Seevers for determinations of the staphylinids and for his suggestions on the phylogeny of these beetles and on their association with the army ants. The vast majority of these beetles does not show any of the morphological specialization typical of most myrmecophilous staphylinids found within colonies of Ecitonini. Some genera, such as *Erchomus*, are similar enough to known myrmecophiles like *Vatesus* that in the field one has to look carefully to avoid possible confusion. Unfortunately more than 25 species of staphylinids, including those which are most abundant within the refuse deposits, can be reliably identified only to the tribes Myrmedoniini and Athetini at the present time. In the refuse deposits of the African *Dorylus* (*Anomma*), staphylinids are likewise the most abundant beetles, and they are primarily not the myrmecophilous species and usually not the same genera found within colonies (Collart, 1934; Paulian, 1948). There are several exceptions in that *Demera* Fauvel in Africa and *Ecitopora* Wasmann and *Tetradonia* Wasmann in the Neotropics are common both in booty refuse, columns and bivouacs. Less common genera found in the refuse deposits of Ecitonini on Barro Colorado Island and not considered to be myrmecophilous include: *Atheta* Thomson, *Coproporus* Eichelbaum, *Echiaster* Erichson, *Erchomus* Motschulsky, *Heterothops* Stephens (with *E. hamatum*), *Hoplandria* Kraatz, *Lispinus* Erichson (with *E. vagans*), *Megalopinus* Eichelbaum, *Philonthus* Curtis, *Staphylinus* Linné, and *Xantholinus* Dejean. The above genera were all taken in refuse deposits of *burchelli* except where another army ant is indicated. The genera *Erchomus* and *Staphylinus* were also found by Wheeler in a cluster of *E. hamatum* on Barro Colorado Island but were not considered "true guests" (Mann, 1925: 166).

It is clear that there is a large complex of species in *Zyrus*, *Drusilla*, and perhaps other closely related genera of Myrmedoniini. Some of these species are myrmecophiles living within the nests of army ants and other ants while others are found in refuse deposits or in habitats not associated with ants. Apparently the species within this broad *Zyrus*-*Drusilla* complex which are myrmecophiles are more common within the refuse deposits than any of the other myrmecophilous Staphylinidae except *Tetradonia*. Some of the species within this complex which are not found within the nests of *E. burchelli* or along the ant columns are the most common species of staphylinids in refuse deposits. The myrmecophilous *Tetradonia* (Aleocharinae) was seen to kill and feed on active army ant workers in refuse deposits and along raid and emigration columns. It also feeds on booty refuse and presumably eats booty within the bivouacs. (More information on Tetradonia and other myrmecophilous Staphylinidae will be given below under beetles found within nests.) The species of Myrmedoniini which are smaller than Tetradonia and which are more common in refuse deposits were seen to attack only weak or dead workers.

The Staphylinidae associated primarily with the refuse deposits were most active at night although they could be seen at any hour of the day. It seemed that during and just after twilight the number of these beetles increased rapidly in the refuse deposits. Counts were made of the number of beetles flying up and down through a flashlight beam held horizontally above a refuse deposit. These indicated that perhaps 120 staphylinids flew to a refuse deposit in 30 minutes. Many of the beetles within the refuse deposit frequently flew short distances above the refuse, but most of these returned immediately. On the surface of the refuse deposit we could often see close to 100 beetles in an area of 150 square centimeters. Almost all samples taken from refuse deposits were collected during the daytime when the population of these beetles had decreased. At least five per cent of the staphylinids were usually lost because they flew so readily when the refuse was collected and placed in Berlese funnels. A sample which yielded 735 staphylinids was taken from refuse deposit nne2 (figure 66) at the statary bivouac site of colony '55 B-IV on 4 March 1955, the first nomadic day. The booty refuse had a volume of about 250 ml. and had been placed there primarily within the preceding 24 hours. Moreover, all the refuse from this same deposit had been collected two days previously. This earlier collection was at least twice as large but included only 202 staphylinids. The large difference in the number of these beetles is attributed to the age of the refuse. The pieces of refuse which are most recently added to a deposit have the maximum amount of food remaining in them and probably have the strongest odor which attracts more beetles. When a refuse deposit was observed once or twice daily for several days without collecting any myrmecocoles or refuse, there was a notable decrease in number of staphylinids during the first 24 hours after the ants ceased visiting the refuse deposit regardless of whether or not the colony was still bivouacked at the site. It is roughly estimated that 90% of the staphylinids left a refuse deposit during the first 24 hours after abandonment, and after 48 hours only an occasional beetle could be seen.

The predominating species of Staphylinidae found in the refuse deposits were constantly running on and below the surface. They did not appear to do much digging but could easily penetrate one to two centimeters beneath the surface layer of refuse and partially into the soil below. The numerous staphylinid and dipterous larvae in the refuse deposits may have done the digging which loosened the soil beneath the refuse itself. Probably most of the staphylinid larvae belong to adults which were common within the refuse, but some of them may be larvae of the myrmecophilous staphylinids because only a few larvae of myrmecophilous insects have ever been found within colonies. Both the adult and larval staphylinids were seen feeding on the dipterous larvae but not on beetle larvae in the refuse deposits.

The following species of Staphylinidae have been reported from refuse deposits of army ants (other species reported as myrmecophiles taken with these ants probably should be included in this category): *Acanthodonia argentina* Bruch (1923: 184-185), *Lithocharodes fuscipennis*

Sharp (Bruch, 1919: 582).

The following species were found in refuse deposits of *E. burchelli* on Barro Colorado Island unless other data are given. Only identified species or genera known to be myrmecophilous and also found in the refuse deposits are listed here. Additional genera not likely to be myrmecophiles have been listed above in the first paragraph under Staphylinidae.

Ecitophya bicolor Reichensperger. Found running in refuse deposit of *E. burchelli*: 2 March 1955 between 8:30 and 10:00 a.m. (1); in emigration columns (2).

Ecitopora fernandi Reichensperger. Found in refuse deposit of *E. burchelli*: 30 January 1955 (3).

Ecitopora n. sp. Over 100 specimens were taken in refuse deposits of *E. burchelli* between 30 January and 20 May 1952, 1955 and 1956. These staphylinids flew readily when I attempted to collect specimens or samples of booty refuse. At least 50 specimens were seen at times flying over refuse deposits in the evening between 5:30 and 7:00 p.m. Although this species was found in the refuse deposits at all times of day, it was most numerous on the surface in the early evening and apparently went deeper into the refuse deposits or soil after midnight. *Ecitopora* sp. was never taken in any ant column but was found in two samples of workers taken from bivouacs. In both cases these bivouac samples were large ones including some detritus from the periphery of the bivouac. *Ecitopora* sp. appears to be most active in the evening when it can find the maximum amount of booty refuse near nomadic colonies. Since it does not emigrate with the army ants, it must fly to new bivouac sites nightly unless it finds a statary colony.

Tetradonia marginalis Reichensperger. There is still some doubt about the identification of all the specimens of *Tetradonia*. About 50 specimens taken on Barro Colorado Island with *E. hamatum*, *burchelli* and *vagans* have been tentatively referred to *T. marginalis*. *Tetradonia* is one of the most common genera of myrmecophiles, and it will be discussed more fully below. *T. marginalis* captures adult army ants around the periphery of bivouacs and along refuse columns and in refuse deposits. Since it can follow the chemical trails of the army ants, it can run along the refuse trails when no ants are present and find the refuse deposits where it will eat or carry off the dead or dying workers.

Tetradonia prosequens Reichensperger. This species probably has habits similar to *T. marginalis*, but *prosequens* was never positively identified as the species seen attacking workers of *hamatum*. Unlike *marginalis* which is found with several hosts, *prosequens* has been found only with *hamatum*. Similar host specificity was reported by Reichensperger (1935: 215-216) based on specimens from Costa Rica. About 65 specimens were taken between 21 February and 29 July.

Pselaphidae: Many species of Pselaphidae have been reported to be associated with different kinds of ants including army ants. However, I know of no incontrovertible evidence that a single species is a myrmecophile. The following species (determined by O. Park) were taken in refuse deposits or bivouac sites of *E. burchelli* or *E. hamatum* on Barro Colorado Island. Other areas in which the species were taken, but where no army ants were present, are also given.

Barroeuplectoides zeteki Park. Bivouac site of *E. burchelli*: 20 January 1955 (1); refuse deposit of *burchelli*: 5 March 1955 (1); forest floor litter: 12 February 1955 (1), 11 March 1955 (5), 30 July

1956 (4), 4 August 1956 (1); Berlese extraction of rotten wood and detritus from inside log: 7 July 1956 (1).

Batrybraxis panamensis Park. Bivouac site of *E. burchelli*: 7 March 1955 (3); bivouac site of *hamatum*: 29 July 1956 (1).

Dalmonexus seeversi Park. Refuse deposit of *E. burchelli*: 5 March 1955 (3).

Jubus turneri Park. Refuse deposit of *E. burchelli*: 26 February 1955 (1); forest floor litter: 10 February to 11 March 1955 (4), 21 July to 15 August 1956 (7); bark, moss and lichens: 27 July 1956 (1).

Melbamina sp. Berlese extraction of empty cocoons, dirt, wood detritus under site of bivouac of *E. burchelli*: 5 March 1955 (2).

Histeridae: About 185 Histeridae were found in the refuse deposits of *E. burchelli* during this survey. The majority of these, like the Staphylinidae, are not myrmecophiles in the strict sense but were found only in the refuse deposits. They may be found in forest floor litter or in refuse from ants of other subfamilies. However, material from refuse deposits of *Atta cephalotes* and samples of detritus from the forest floor and tree holes or rotten logs did not reveal any of the same species. Although some of the histerids found in refuse deposits are included in the emigrations, most of them apparently fly from one refuse deposit to another. The species found in refuse deposits are listed alphabetically below including published records. The strictly myrmecophilous species, preceded by an asterisk, were also found within bivouacs or in columns, and will be discussed more fully in a later section. The determinations have been made by Rupert L. Wenzel. The following list is based on about ten per cent of the specimens collected.

***Alloiodites* n. sp. In refuse deposit of *E. burchelli*: 12 May 1956 (1♀); in emigration column of *L. praedator*: (1♂).

Bacanius sp. In sample of dirt and workers from bivouac of *E. dulcius crassinode*: 4 July 1956 (1♂).

**Cheilister lucidulus* Reichensperger. Found in refuse column of *E. burchelli*: 3 May 1956 (1 sex?).

Epierus schmidti Wenzel and Dybas. In refuse deposit of *E. burchelli*: 12 May 1956 (1♂, 1♀).

**Mesynodites* Reichardt. About 50 species of *Mesynodites* have been found with army ants, and several additional species have been found with nondoryline ants or in detritus. Some of the species can be considered myrmecophiles since they ride on the ants and live in the bivouacs of army ants. Most of the species appear to be found primarily in the refuse of the colony, and a few may be found only there. These beetles sometimes remain at the bivouac site or in refuse deposits after the colony emigrates, and it is probable that they get to new colonies by flying rather than by running along the old chemical trails of the ants. Only the species clearly reported from refuse are listed here along with those found in refuse deposits on Barro Colorado Island. Unfortunately, most authors have reported that specimens were found in "nests" or have given only the name of the host.

**Mesynodites ciliatus* Bruch. Found in refuse deposits, bivouacs and columns of *E. dulcius dulcius* in Argentina and Brasil (Bruch 1923: 181, 191-192; 1926a: 8; 1926b: 20; 1928: 352; 1934b: 261-262) and with *Neivamyrmex pertyi* (Shuckard) in Argentina (Bruch, 1929: 433). More than 300 specimens were collected at the entrance of a nest abandoned two days earlier by a colony of *dulcius s. str.*, and none were seen during the emigration of this colony which was watched at different times (Bruch, 1926b: 18).

**Mesynodites confirmatus* Reichensperger. In refuse deposits of *E. burchelli*: 30 January 1955 (1), 2 February 1955 (1 sex?, 1♀); in emigration of *burchelli*: (1♀).

**Mesynodites ecitonis* Bruch. Found in refuse deposits and reported from nests of *E. vagans*, *E. dulcius dulcius*, *E. mexicanum* and *Neivamyrmex pseudops* in Argentina and Brasil (Bruch, 1923: 181, 190-192; 1926a: 8; 1926b: 18; 1928: 352; 1929: 433; Reichensperger, 1938: 81, 91). Many specimens were taken apparently among refuse at the entrance of a nest of *dulcius dulcius* abandoned two days earlier (Bruch, 1926b: 18).

**Mesynodites geminus* Reichensperger. Found in refuse deposit of *E. burchelli*: 9 May 1956 (1); reported from "nest" of *burchelli* in Costa Rica (Reichensperger, 1935: 193-194).

Mesynodites major Bruch. Found in refuse deposit of *E. dulcius dulcius* in Argentina (Bruch, 1923: 181, 189-190; 1926a: 8).

**Mesynodites obscurus* Reichensperger. Found chiefly in the detritus of the bivouacs but also found in columns of *Labidus praedator* and *L. coecus* in Costa Rica and Brasil (Reichensperger, 1939a: 119-122).

**Mesynodites reticulatus* Bruch. In refuse deposits of *E. dulcius dulcius* in Argentina (Bruch, 1926a: 8-9).

Omalodes gagatinus Erichson. Attracted to area of soil and refuse dug from around bivouac of *E. vagans* as well as to workers milling around on ground after the bivouac was dug up: 9 July 1956 (5 taken, 7 seen).

**Paratropinus scalptus* Reichensperger. In refuse deposits of *E. burchelli*: 2 March 1955, 8:30 to 10:00 a.m. (2), 20 February 1956 (1♂), 23 May 1956, on second nomadic day in refuse deposit at statary bivouac site (1♂); also reported from column of *burchelli* in Costa Rica (Reichensperger, 1935: 199-200).

Phelister n. sp. In refuse deposit of *E. burchelli*: 15 May 1956 (1♀).

**Phelister sculpturatus* Schmidt. In refuse deposit of *E. burchelli*: 9 May 1956 (1); reported from Costa Rica with *L. praedator* (Reichensperger, 1939b: 280).

Phelister williamsi Wenzel and Dybas. In dirt, leaves, detritus and booty refuse from under and around position of bivouac of *E. hamatum* on approximately sixth nomadic day but sample taken three days later after colony left this site (1♀).

Psalidister n. sp. 1. In refuse deposits of *E. burchelli*: 28 February 1955 (1♀), 2 March 1955 (1♀), 17 March 1955 (1♀), 20 February 1956 (1♂, 2♀).

Psalidister n. sp. 2. In refuse deposit of *E. burchelli*: 12 May 1956 (1♀).

**Psalidister burchelli costaricensis* Reichensperger. In refuse deposit of *E. burchelli*: 20 February 1956 (1♂); also taken in an emigration; reported from Costa Rica with *E. burchelli* (Reichensperger, 1935: 190, 198-199).

Saprinus n. sp. In refuse deposit of *E. burchelli*: 12 May 1956 (1).

Troglosternus ecitonis Mann. In refuse deposits of *E. hamatum*: 23 June 1956 (2♂, 1♀). One pair was taken as they were copulating while running around in refuse deposit under site of bivouac at 10:30 p.m. just after last ants had emigrated. These beetles were still *in copulo* on following morning at 9:00 a.m. *T. ecitonis* has also been found with *L. coecus* (Reichensperger, 1935: 209).

Scarabaeidae: Although at least two genera of Scarabaeidae, *Alloscelus* and *Caccobius* Thomson, have been found associated with African colonies of *Dorylus* (*Anomma*) (Kohl in Wasmann, 1904: 668; Cohic, 1948: 269; Collart, 1934: 240), I know of no reports of this family being found with Ecitonini. Since the odors of the refuse deposits and bivouacs of *E. burchelli* have been compared with excrement and rotting insects, one might expect dung beetles would be attracted to them. However, only a few species were found, and these were quite rare. Less than 20 specimens were taken, and three species which may be attracted to the refuse deposits on Barro Colorado Island are listed here. F. S. Pereira determined these specimens, and the remaining scarabaeids have not yet been determined.

Deltochilum parile Bates. 23 March 1956 (1).

Glaphyrocanthon lampros (Bates). 28 March 1956 (1).

Onthophagus dicranius Bates. 28 March 1956 (1).

Hymenoptera

Diapriidae, the most important family of myrmecophilous Hymenoptera found within colonies of Ecitonini, are also represented in refuse deposits. However, nondoryline ants are the most abundant group of Hymenoptera in number of individuals found in the booty refuse. In addition, one specimen of *Ceraphron* sp. (Ceraphronidae) (determined by C. F. W. Muesebeck) was found in a refuse deposit of *E. burchelli*. At least two species of ceraphronids, *Ceraphron croceipes* Brues and *Ecitonetes subapterus* Brues (1902: 369-371), have been found in bivouacs of army ants. *Epiencyrtus* sp. (Encyrtidae) was found in a bivouac site of *E. hamatum*; the known hosts for this genus are Ichneumonidae (B. D. Burks, in letter).

A new genus of Chalcididae, *Litus* sp. (Mymaridae), *Spalangia drosophilae* Ashmead (Pteromalidae), *Horismenus* sp. (Eulophidae), and a new genus of Encyrtidae (all determined by B. D. Burks) were found in refuse deposits of *E. burchelli* on Barro Colorado Island. *S. drosophilae* is known to be parasitic on a variety of small Diptera and Hymenoptera (*Drosophila*, *Siphona*, *Alysia* and *Eucoila*) (Muesebeck, *et al*., 1951: 535). Probably most of these wasps are parasitic on Diptera which breed in the refuse deposits in large numbers.

Cynipoidea: Cynipoid wasps were quite abundant in refuse deposits of *E. burchelli* where they probably are parasitic on puparia of Diptera. The following species (determined by L. H. Weld) were found on Barro Colorado Island.

Emargo eciton Weld. This genus and species of Figitidae (Figitinae), described by Weld (1960), was the most abundant cynipoid found in refuse deposits. Twenty females and one male were taken between 30 January and 28 March in refuse deposits of *Eciton burchelli*. One other species of Figitidae, *Xyalophora pilosa* Borgmeier (1935: 103-104), has been reported associated with Ecitonini (*Nomamyrmex hartigi*).

Pseudeucoila (*Tetramerocera*) sp. (Cynipidae: Eucoilinae). In refuse deposits of *E. burchelli*: 28 February to 1 March 1955 (3).

Trybliographa (*Hexaplasta*) sp. (Cynipidae: Eucoilinae). In refuse deposits of *E. burchelli*: 30 January to 17 March 1955 (16), 28 March 1956 (2). One species, *zigzag*, is known to be parasitic on a phorid (Muesebeck, *et al*., 1951: 603).

Trybliographa (*Tetraplasta*) sp. In refuse deposits of *E. burchelli*: 17 February 1955 (1), 23 March 1956, found dead inside puparium of cyclorraphous fly, (1).

Diapriidae: Diapriidae are known to be parasitic on flies of several families, and I know of no evidence that any of the myrmecophilous species is parasitic on any ant. None of the following species taken on Barro Colorado Island was seen alive, and it is not known whether any of them are myrmecophiles.

Diapriinae sp. 1. Reared from fly puparium (1453) found in laboratory nest of *E. hamatum*, 17 March 1956 (1)

Doliopria n. sp. In refuse deposit of *E. burchelli*: 30 January 1955 (1); flying near bivouac of *E. burchelli*: 20 February 1956 (1).

Doliopria spp. have also been reported associated with army ants in Brasil and Bolivia (Ferrière, 1929; Borgmeier, 1939).

Phaenopria magniclavata Ashmead. In refuse deposits of *E. burchelli*: 30 January to 16 March 1955 (165); Berlese sample of detritus from forest floor: 11 March 1955 (1).

Trichopria spp. In refuse deposits of *E. burchelli*: 30 January to 5 March 1955 (9), 17 February 1956 (1); over swarm raid of *E. burchelli*: 12 February 1955 (3); in raid column of *Labidus praedator*: 15 March 1956 (1); in raid column of *Neivamyrmex humilis*: 26 July 1956 (1). The latter two wasps are not the same species as those found with *burchelli*. These wasps were not seen in the columns but were found in samples of preserved ants aspirated from the columns. Flies of various families are known to be hosts for these parasites (Muesebeck, *et al*., 1951: 678-680). I know of no other records of finding this genus with Ecitonini. At least some species of *Trichopria* and *Doliopria* probably emigrate with the army ants and should be considered myrmecophiles.

Bethylidae: "The members of the family Bethylidae attack almost exclusively the larvae of Lepidoptera and Coleoptera, thus showing an exceptional uniformity in host preferences" (Clausen, 1940: 308). Thus, one would expect that the bethylids found with army ants are most likely parasites on Coleoptera associated with the ants rather than on the ants themselves. Two specimens of Dissomphalus Ashmead were found in refuse deposits of E. burchelli, and a specimen close to Rhabdepyris Kieffer was taken over a swarm raid of burchelli. The latter genus includes at least one species reported to be a myrmecophile, and other bethylids have been found in columns of Ecitonini.

Formicidae: There is no evidence that any species of nondoryline ant has any type of symbiotic relationship with army ants. Nevertheless a number of species are commonly found raiding the booty remains in the refuse deposits of the army ants. A few species attack active or weak workers of burchelli in the refuse deposits or columns. Some of the species are attacked by the army ants, but most species seem to avoid contact with the army ants or are too small to be attacked by the dorylines. The following ants (determined by W. L. Brown, Jr.) were found in refuse deposits of E. burchelli on Barro Colorado Island. It is possible that most carnivorous ants forage at times in refuse deposits.

Anochetus mayri Emery. Found foraging in refuse deposits.

Azteca spp. Often carried off booty refuse and occasionally removed dead burchelli workers. At one refuse deposit Azteca workers carried off more than 12 pieces of booty in five minutes. This genus also attacks living beetles in the refuse deposits. On one occasion a major worker of E. hamatum was captured by 26 workers of Azteca. The major was alive but may have been injured before it was attacked.

Camponotus buttesi Forel. Found in a refuse deposit of E. burchelli.

Ectatomma ruidum Roger. Foraged in refuse deposits of *E. burchelli* and carried away dead army ant workers.

Erebomyrma sp. Found in refuse deposits of *burchelli*.

Gnamptogenys tornata (Roger). Found in refuse deposit of *burchelli*.

Mesoponera arhuaca (Forel). Found in refuse deposit of *burchelli*.

Mesoponera constricta (Mayr). Found carrying living larvae of *Euryomma* (Faniinae) away from refuse deposits.

Neoponera striatinodis (Emery). Captured a small active intermediate worker at the edge of a bivouac of *E. burchelli*.

Neoponera theresiae (Forel). Captured active intermediate workers of *burchelli*.

Neoponera villosa (Fabricius). Found in refuse deposit of *burchelli*.

Pachycondyla harpax (Fabricius). Found in refuse deposit of *burchelli*.

Pheidole spp. Frequently found taking remains of booty from refuse deposits of *burchelli* and also seen at bivouacs of *hamatum* and *vagans*. Pheidole was not seen to capture any worker army ant, but it attacked *burchelli* workers causing them to retreat from parts of refuse deposits. *Pheidole* also blocked the advance of raid columns of *hamatum*, *Neivamyrmex* and *Labidus*. No *Pheidole* workers were seen among any of the army ant booty.

Ponera sp. Found in refuse deposit of *burchelli*.

Proceratium micrommatum (Roger). Found in refuse deposit of *burchelli*.

Solenopsis (*Diplorhoptrum*) sp. Found in refuse deposits of *burchelli* where it was apparently foraging.

Strumigenys gundlachi (Roger) and *S. subedentata* Mayr. Found in refuse deposits where they appeared to be attracted in larger numbers than in surrounding litter; they probably were capturing Collembola or other microarthropods in the refuse deposits.

Apidae: *Meliponinae*: Some species of stingless bees are noted for their habits of eating or collecting pitch of trees, rotting fruit or vegetation, dead carcasses, and dung. Since the odor of the refuse deposits of *burchelli* is strong and reminiscent of rotting insects, one might expect that these stingless bees might be attracted to the booty refuse. The stingless bees which I frequently saw and collected at excrement and dead carcasses on Barro Colorado Island belong to six species of *Trigona* (determined by Herbert F. Schwarz). However, the only species seen to visit refuse deposits of *E. burchelli* is *Melipona marginata micheneri* Schwarz. These workers on two occasions were clearly seen to feed on the booty refuse. No species of *Trigona* was ever seen at the refuse deposits.

MYRMECOCOLES FOUND IN BIVOUACS AND COLUMNS OF ARMY ANTS

Arthropods collected from columns of army ants or taken in samples of ants from bivouacs have usually been called "ecitophiles" or "myrmecophiles" in the literature. When collecting from columns or bivouacs, one invariably finds arthropods which are not myrmecophiles. These are usually booty or arthropods picked up accidentally from the dirt or debris next to the ants. Therefore, in this section specimens whose association with the ants is more doubtful will be called myrmecocoles. The terms myrmecophile and inquiline are used interchangeably here for those species which: (1) run in a column of army ants; (2) ride on the ants; (3) ride on any arthropod or object carried by the ants; (4) are ectoparasitic on the ants; and (5) are carried by the ants (and are not booty). In addition, systematic or taxonomic relationships combined with morphological specialization are used to determine whether an arthropod is a myrmecophile. However, in all cases, even though it may be repetitious, the best available behavioral information will be given to support the use of the term myrmecophile. A complete catalog of myrmecophiles associated with army ants is impractical at this time, but a fairly complete list of major groups, genera, and known fragments of biology or behavior will be included. Unfortunately, most published records include only the name of the host and ambiguous statements, such as that an insect was taken "in a column." Information on myrmecophiles is so difficult to obtain that every effort should be made to report accurate observations however insignificant they may seem by themselves.

Since there is no substantiated case of a myrmecophile being found in bivouacs and not found in columns, those arthropods found in either location will be considered together. Generalizations regarding genera or other supraspecific taxa will be given at the beginning of the discussion of each group. More comprehensive summaries will be given at the end of this systematic survey.

Araneida

No myrmecophilous spiders were found on Barro Colorado Island, but two species may be inquilines in colonies of army ants. Fage (1938) reported five species of spiders from nests of *Labidus praedator* and *Eciton hamatum*, but these are almost certainly free-living forms from detritus collected with the ants.

Brucharachne ecitophila Mello-Leitão. The family Brucharachnidae was based on *Brucharachne ecitophila* Mello-Leitão (1925: 234-237), but this species was subsequently placed in Oonopidae by Fage (1938: 369). The species was taken with *Neivamyrmex raptans* (Forel) and *Wasmannia auropunctata* v. *australis* Emery at Córdoba, Argentina. The femora have apophyses with trichomes or hairs which may have a secretion attractive to ants (Mello-Leitão, 1926: 2). The lack of eyes may be an adaptation for a subterranean or myrmecophilous life, and Bruch (1929: 437) considers this spider to be an inquiline.

Myrmecoscaphiella borgmeyeri Mello-Leitão. *Myrmecoscaphiella borgmeyeri* was found in the nest of *Eciton* sp. [*s. lat.*] in Brasil (Mello-Leitão, 1926: 1-2). It was placed in the family Oonopidae by Fage (1938: 369-370). The palpi of this spider have hairs which may be trichomes.

Acarina

There appear to be at least as many species of myrmecophilous mites as there are species of insects found with Neotropical army ants. However, only about 12 species of mites have been described from these ants. As in most other groups of inquilines, many of the mites also seem to be highly specialized morphologically for living in the ant colonies. Most of these unusual species of Acarina are adapted for riding on the ants. This survey includes only a small fraction of the mite fauna from the Ecitonini, but it is an adequate sample to show that some species are restricted to one or a few hosts, whereas other species are found with a number of hosts.

The small size of the mites is probably the primary reason why so few species have been previously collected and described. The techniques discussed under the section on methods for collecting myrmecocoles can be used for mites. However, some modifications of collecting and sorting techniques will greatly increase the number of mites found in samples. It is extremely important to collect the ants with a minimum of dirt or debris. When there is dirt mixed in a sample of ants, not only does it stick to the mites, but it makes sorting much slower. Moreover, many nonmyrmecophilous species of mites are introduced into the sample with the dirt.

When collecting ants for the recovery of mites it is also important not to pour off the preserving fluid without filtering it or carefully examining it under a microscope. Many of the species of mites are too small to be easily seen without some magnification, and they can be lost by decanting the preserving fluid.

The sorting of preserved samples is done most effectively by using clear petri dishes or watch glasses. These can be placed over both white and dull black backgrounds and also can be examined by transmitted light reflected from a mirror below the stage of the microscope. Transmitted light is especially useful when sorting samples of eggs and larvae of ants. These immature stages are normally somewhat translucent when preserved in alcohol. Mites can often be seen if they are under larvae, and mites which mimic the eggs or larvae are normally much denser or darker than the brood.

The mites associated with the army ants can be divided into two ecological groups: (1) those species that are found in the refuse deposits, and (2) those species found on the ants themselves or within the bivouac. Because there is little duplication of species in these two groups, the ones found primarily in refuse deposits have been considered above in the section on the refuse deposits. Most of the mites from these areas where the ants drop the remains of their booty are probably not myrmecophiles. They seem to be common throughout the forest floor litter and only become more abundant in areas of booty refuse because of the rich source of food there.

Samples of ants almost always contain some species of mites that most probably are not inquilines. These are not included in this paper except where some association with the ants is known or suspected. Many similar "myrmecophilous mites" recorded in the literature with ants are undoubtedly not myrmecophiles. Nevertheless, a number of mites have been included in this discussion even though the only evidence that they are myrmecophilous is their taxonomic relationship to known inquilines.

The mites will be considered in the systematic order as given by Baker, et al. (1958). Within the families, genera will be listed alphabetically. Since almost all these mites are new species, within each family the mites will be listed by arbitrary species numbers without regard for any systematic position below the family level. Where two or more species appear to be closely related within a family, these have usually been grouped as "genera". Thus, circocyllibanid A-1 and A-2 are considered to be two species more closely related than either is to circocyllibanid B-1 or B-2. Further study may show that species A-1 and A-2 should not be considered to belong to a new genus but rather would be better treated as a subgenus or some other taxon. However, for the present, the terminology used will provide some information on relationships within the families which is useful for discussion of host specificity.

Almost all the "species" have been based on material mounted on microscope slides. Approximately 5,000 slides were examined, and the remainder of the mites have been kept in alcohol and sorted as completely as possible with a stereoscopic microscope (1X to 80X magnification). Temporary slide mounts in glycerin were made in some cases. Specific identification of these myrmecophilous mites in alcohol seems to be reliable for most of the larger species such as the Mesostigmata. The large amount of morphological specialization makes this sorting easier than with most free-living mites. In no case was the species of host used as the sole criterion for determining a species of mite.

A summary of the number of worker ants examined for each species of army ant is given in tables 3 and 4. These tables also give the total number of colonies sampled and the number of colonies from which at least 50 ants were examined. If the mites were evenly distributed among the samples included in this survey, samples of 50 ants would have 0.5 to 1.0 mites in them. By comparing colonies from which at least 50 ants were examined, many small ant samples are eliminated. Summaries of the number of mites collected with each host are given for most of the species of mites in tables 10 to 12. In these tables under the number of specimens of each species of mite found with each host the number followed by "c" indicates the number of colonies in which that mite was found.

Taking samples from several different parts of a colony may give a better yield of mites than taking a single sample of equivalent total number of ants. Separate samples were usually taken from a bivouac, a raid column, or an emigration column. There have not been enough samples taken from these various places to show whether mites are more apt to be present on workers in bivouacs than in raid columns. However, in a few special cases, such as the mites that mimic ant larvae, it is almost certain that these mites would be present only where the ant larvae are present, *i.e.*, usually in the bivouacs or emigration columns.

Parasitoidea

About 20 species of nymphal Parasitoidea were found in ant samples, but most of these were represented by only a few specimens. Only the few which appear to be associated with the ant colonies directly or indirectly are considered here. It is unlikely that any of these nymphs are immature stages of any of the adult mites found with the ants.

Parasitoidea species A-1: One of the species which has been found most freqnently is represented by a deutonymph belonging to the

Neoparasitidae or a closely related family. This deutonymph is distinctive because of the unusually broad, blade-like dorsal setae and the broad, short, peg-like ventral setae. No adults or other instars which look as if they could belong to this species were found in the refuse deposits or ant samples.

Parasitoid A-1 has been found in at least 17 colonies of *Eciton burchelli* but with no other host except for one specimen taken with *Labidus praedator*. This single exception was found in a sample of 7,550 workers. A total of over 25,000 workers of *praedator* was examined without finding additional specimens. The similarity in raiding behavior of these two species of ants may be connected with the finding of this mite with both hosts.

It is noteworthy that even though *E. hamatum* is considered to be the species most closely related to *burchelli* on both morphological and behavioral grounds, examination of over 30,000 workers of *hamatum* has not revealed a single specimen of parasitoid species A-1. Not only was this mite found in all large samples of *burchelli foreli* taken on Barro Colorado Island, but it was also found in a sample of *E. burchelli cupiens* taken in British Guiana by Dr. Neal A. Weber (colony D-137). A total of 72 specimens of parasitoid genus A were found in a sample of 10,000 to 15,000 workers taken from this colony. Twenty-four of these mites were mounted on slides, and six of these could not be distinguished from specimens taken in Panamá. The other 18 mounted specimens belong to a second species A-2. The remaining 48 specimens could not be reliably identified in alcohol. These two species, parasitoid A-1 and A-2, are among a series of examples in which either the same species or distinct but closely related species of inquilines are found with the same species of host from widely separated localities.

Parasitoid species A-1 must be found on adult workers, since it is found in samples with no brood. However, its exact position on the ants, and whether or not it is parasitic are unknown.

Parasitoidea species A-2: This species is represented only by deutonymphs from a single sample of *E. burchelli cupiens* collected in British Guiana (colony D-137); it is discussed more fully under species A-1 above.

Parasitoidea species 30: This large species, represented by deutonymphs, probably is a parasitid or neoparasitid. No other instars were found which appear to be closely related. Parasitoid species 30 has been found in samples of four species of ants: *E. hamatum*, *dulcius*, *vagans* and *mexicanum*. However, this deutonymph was never found attached to an ant. Most specimens were attached to the abdomens of Phoridae, and the remainder were free in the vials. Unlike most of the mites found in the ant samples, these deutonymphs often remained on the host flies when they were killed in alcohol or Bouin's fixative. Normally a single mite is attached to the abdomen of the phorid near the thorax, but a single phorid may have as many as eight mites on it. These mites are considered parasitic because their chelicerae are inserted through the body wall of the phorid. After this species has dropped off the phorid, a small spot is visible in the membrane where each mite was attached. Parasitoid species 30 probably is not directly associated with the ants.

This mite has been found on four species of *Ecitophora* (Phoridae). Inasmuch as other species and genera of Phoridae were found with the same army ants, it is evident that the mites do not attach at random to any phorid within the colony or in the refuse deposits. These mites were found on the following species of *Ecitophora* (respective ant hosts given in parentheses): *bruchi* Schmitz (*mexicanum*), *collegiana* Borgmeier (*hamatum* and *mexicanum*), *pilosula* Borgmeier (*dulcius*), and *varians* Borgmeier (*vagans*).

Parasitoidea species 32: The above discussion of Parasitoidea species 30 also applies to this second species found on Phoridae. However, this species is scarcer and was found only with *E. hamatum* and *burchelli*. It was found only on *Ecituncula tarsalis* Borgmeier, a phorid taken only with *hamatum* and *burchelli*, primarily in the refuse deposits.

Macrochelidae

The family Macrochelidae includes two or three genera and three undescribed species which are considered myrmecophiles with Ecitonini. Two of these species are ectoparasites. The third species is thought to be a myrmecophile only because it was found with two colonies of the same host and is morphologically very different from other macrochelids.

Macrochelidae species 2: This species probably belongs to a new genus of Macrochelinae. It is possibly unique among all the Macrochelidae in that the fourth pair of legs are thicker than any other pair. In all other species of Macrochelidae that I have seen (more than 30), the second pair of legs is the thickest. In macrochelid species 2 the first, second and third pairs of legs seem to have the proportions found in other macrochelids with the second pair thicker than the first and third pairs. For the size of the mite, the lengths of all the legs appear to be the same as those of other members of the family. Many of the plumose setae, that are frequently found on the dorsum and venter of macrochelids, in this species are tree-like with only a few unusually long branches.

A total of 23 females was found with three colonies of E. dulcius, making a ratio of 1:209 ants. At least six of these mites were found attached to the hind tarsi of majors or large intermediate workers. These mites are large enough that the first specimens discovered were seen on an emigration column at night. The lump at the tip of the hind leg of a major was mistaken for a piece of dirt when first seen. All the mites that were found attached had their chelicerae inserted in the small membrane between the tarsal claws of hind legs. The palpi may help hold the mite on the tarsus. Although the first pair of legs of the army ant is smaller than the others, there is a much larger membrane between the claws of the front tarsi. However, none of the mites was found on the first or second pairs. Inasmuch as the exact location on the ant is known for only about six mites, additional records may show that this mite is not so highly restricted to the hind legs.

Figure 15 shows one of these mites attached to a hind tarsus contrasted with the last tarsal segments without a mite. In this photograph of living specimens, the large, curved hind legs of the mite are easily seen. The mite was always found with its hind legs curved as shown in figure 15. In small laboratory nests these ants sometimes hooked their legs on other ants or the side of the nest by means of the hind legs of the mites. Not merely the tarsal claws of the mite, but both entire hind legs served as claws. In fact, this behavior seemed to be more common for the leg with the mite than the use of the ant's own tarsal claws. At times an ant would keep its leg hooked on an object by means of the mite's legs for several minutes without moving. This behavior indicates that contact or pressure on the tarsal claws is not necessary in order for an ant to keep a leg in a fixed position. The stretching of the leg is probably more important for the immobilization of the ant which is essential for the formation of hanging clusters. We were not able to observe the behavior of dulcius workers with this macrochelid in hanging clusters or "ropes of ants" such as are found in bivouacs. The mites stayed on the same ant leg for at least two days in the laboratory. Probably with better laboratory conditions and less handling of the ants, the mites would have remained on the tarsi longer. When an ant was killed by pinning it down for photographing the mite, the macrochelid left the ant in a few minutes. The mites also detached when the ants were put in alcohol.

Macrochelid species 2 appears to be a parasite on the larger worker ants. It clearly emigrates attached to the hind tarsi of the ants and seems to be restricted to E. dulcius. Nothing is known concerning the males or any other instar of this species.

Macrochelidae species 3: Macrochelid species 3 also was found attached to the hind tarsi of larger workers, but it was on a different host, E. vagans. The ratio of mites to ants is 1:240. This mite does not have the greatly enlarged hind legs which are found in macrochelid species 2 and differs from it in many other ways. The dorsal and ventral setae have more numerous and shorter branches such as are common in free-living Macrochelidae. No males or other instars were found. Although most of these specimens were found loose in alcohol, more than ten were seen attached to tarsi of living ants. Most of the mites were on majors, but at least two were on hind tarsi of large intermediate workers. Even though this species does not have greatly enlarged hind legs, the workers were seen to hook their legs on supports using the hind legs of the mite rather than their own tarsal claws.

Macrochelidae species 7: A third species of Macrochelidae, species 7, is tentatively considered a myrmecophile, primarily because of its unusual shape. Compared with common macrochelids of the same width, this species is twice as long but shows no obvious modifications for myrmecophily. The second pair of legs is thicker than any of the others. Three specimens of species 7 were found in a sample of *E. burchelli cupiens* taken in British Guiana (colony D-137). An additional specimen was found in a sample of *E. burchelli urichi* taken on Trinidad (colony D-152).

Neoparasitidae

There is one genus (here called genus A), or possibly several closely related genera, which probably belong in the family Neoparasitidae although the palpal claw has only two tines rather than the three typical of the family. All six species are heavily sclerotized mites with similar patterns of large depressions on the dorsum and with heavy sculpturing on the entire surface of the body. Over 98% of the specimens are females, and no immature stages are known. Some of the mites, and especially those from subterranean species of ants, are covered with dirt which is difficult to remove.

This genus ranges from Arizona and Texas to Southern Brasil. Because of the wide geographical distribution and the fact that this genus is found on the four common genera of Ecitonini, many additional species probably remain to be found. The largest geographical range of a species known at present is that for species A-1 known from Panamá and British Guiana.

Over 1,100 specimens of genus A were found but only 25 of these are males. The few times that males of these neoparasitids were found suggest the hypothesis that the life cycle of the mites is correlated with the production of sexual broods of the dorylines. Twenty males of neoparasitid species A-1 were taken in Panamá between 30 January and 5 March 1955 from refuse deposits of colony '55 B-I. The burchelli males are produced at this time of year. Species A-3 males were found in a praedator bivouac with praedator males on 19 March 1952. Species A-2 males were found with vagans males on 7 August 1956. Males and females of both species A-2 and A-3 were most probably on alate males, but they were only discovered after the male ants had been put in alcohol along with some workers. The large numbers of male ants (over 150) and the fact that they all were alates showing little tendency to lose their wings, leads one to believe that these alates must have been found in the colony which produced them. No males of neoparasitid genus A were found with any host at times of the year when the males of the host were not produced. Moreover, a total of 13 females of species A-5 and A-6 have been found on males taken at lights. Thus, males of genus A may be produced before or at the time of appearance of the male ants; this timing would permit fertilization of the females before a dispersal flight. Genus A and Laelaspis are the only myrmecophiles which are known to ride on the male Dorylinae during flight.

Throughout the various groups of inquilines there are repeated instances where the size of a guest or parasite appears to be correlated with the size of the host. This correlation has been mentioned by various authors who have worked on different groups of myrmecophilous insects but apparently has not been suggested for any group of mites. In the neoparasitid genus A there appears to be some correlation between the size of the mite species and the size of the hosts. In comparing the sizes of these mites, the "lengths" have been measured from the anterior edge of the sternal plate to the posterior edge of the ventral plate. The smallest species are A-6 and A-3 found respectively on Neivamyrmex harrisi and L. praedator. The largest species, A-2 and A-5, were found on E. vagans, dulcius and quadriglume which are the largest species of Ecitonini. Species A-4 is intermediate in size and was found primarily on Nomamyrmex esenbecki which is somewhat smaller than the three species of Eciton mentioned. However, species A-4 was also found on L. praedator. It seems to be much rarer with praedator than with esenbecki and also scarcer than species A-3 with praedator. It would be interesting to learn if species A-4 is only found on the largest workers of praedator. Another possible exception to this supposed size correlation is species A-1 which is slightly larger than the species with praedator but is found on burchelli and hamatum which are only slightly smaller than vagans, dulcius and quadriglume. Further observations on additional hosts as well as the behavior on these hosts may help clarify these size correlations. On the male ants the mites are phoretic, whereas on larvae and probably on workers they are parasitic.

Neoparasitidae species A-1: Neoparasitid species A-1 is intermediate in size (length 407μ) among the six species of this genus. It was found on two closely related hosts: E. burchelli and hamatum. However, a relatively larger number of specimens were taken with burchelli (ratio 1:537) compared with *hamatum* (ratio 1:482). A total of 1,104 females of this species was taken from three subspecies of *burchelli* (*foreli*, *cupiens* and *urichi*) and from *E*. *hamatum* (see table 10). Only 20 males of species A-1 were found, and these were all taken in refuse deposits or under the sites of bivouacs where there was some booty refuse. They were found in Panamá with two colonies on five different dates between 30 January and 5 March which is when sexual broods of the host are produced. The dry season also begins at this time, and the dry conditions may be the primary factor in triggering the appearance of the males.

Neoparasitid A-1 was found on over 150 major workers of *burchelli* and over 20 majors of *hamatum*. In these cases it was invariably attached to a small membrane which extends from the underside of the labrum to the base of the mandibles. Many of the ants had one mite on each side of the mouth, a few had two on one side. None of these mites was found on submajors, smaller workers, males or queens. This neoparasitid was also found frequently on the larvae. Although neoparasitid A-1 was found feeding on most areas of the larvae, a distinctly greater percentage of these mites was found attached at the mouthparts of the ant larvae. All attempts to determine exactly how these mites were attached were unsuccessful. The squirming of the larvae indicated that the mites irritated the larvae in this position, especially when first starting to feed. Actual feeding must have taken place since the mites became swollen, distending the membrane between the dorsum and venter. When the mites are feeding at the mouthparts of the larvae it is impossible for the ant larvae to feed. Sometimes after species A-1 had fed on the side of an *Eciton* larva, a darkened disk (more heavily sclerotized?) developed around the site of the puncture. Whether these injuries have any effect on the development of the larvae was not determined. These puncture wounds may be important for stimulating attacks by other myrmecophiles or by the workers. Both the Eciton workers and Histeridae were seen to touch these sites with their mouthparts, but they were not seen to feed there more than a few seconds. Army ant workers will readily attack their own larvae in the laboratory, especially if there is a lack of food. However, they will attack injured larvae more readily than uninjured ones as can be demonstrated by puncturing the larvae with a fine needle. Once they start to feed, the workers are apt to continue until the larva is killed and consumed. Cannibalism is known to occur within the bivouacs in nature, but the extent of this cannibalism is unknown. Perhaps the feeding of the Neoparasitidae and other myrmecophiles is an important factor in initiating this behavior of the ants.

Neoparasitidae species A-2: This species of Neoparasitidae is much larger (length 910-984μ) compared to species A-1 (length about 407μ), and it is also found on larger hosts. Only 19 specimens were found, 14 with E. vagans (ratio 1:970) and five with dulcius (ratio 1:959). One male was found among 14 specimens of A-2 taken with males and workers from an emigration column of vagans. The finding of this one male among only 14 specimens seems remarkable, since not a single male was found among 1,104 specimens of A-1 taken with ants. The location of species A-2 on the ants is unknown, but some of the specimens probably were riding on males since only a few smaller workers were collected with these males from an emigration column.

Neoparasitidae species A-3: Four males and 22 females of species A-3 were found with *L. praedator* (a ratio of 1:938). Therefore, the incidence of this species is about the same as species A-2 and about one-half as great as A-1. Even though the size of the *praedator* workers is much smaller, this mite is less than one-half as large (375μ) as the largest species of genus A. Perhaps it is significant that even though 22 samples of more than 50 ants were examined, A-3 was found only in two samples. One of these was taken from an emigration; the other sample included over 150 male ants taken from a bivouac. The sample from the bivouac included three males of A-3. In the bivouacs and emigration columns of *L. praedator* it is possible to collect larger workers than are normally seen in raid swarms and raid columns. This mite probably could not attach itself to any of the smaller workers and may be restricted to the largest individuals and the males.

Neoparasitidae species A-4: Neoparasitid species A-4 was found in one colony of *Nomamyrmex esenbecki* and two colonies of *L. praedator*. However, 59 specimens were found with the former species (ratio 1:59) and only two with the latter (ratio 1:12,199). Since the specimens with *esenbecki* are all from a single colony, this high incidence may not be typical for the mite with this host. Species A-4 is a large mite (length 803-888μ) which one might expect would be found on larger workers and thus would be more common with *Eciton* or *Nomamyrmex*. The smaller species, A-3, was more common than A-4 on *praedator*.

Neoparasitidae species A-5: This species is known from only two specimens found when a sample of 46 dry pinned males of *E. quadriglume* was examined. These males had been taken at lights in Southern Brasil.

Species A-5 is the largest species (length 1,070μ) in genus A. These two specimens were weakly attached to the hairs of the propodeum, and it is likely that additional specimens may have fallen off before they could be examined.

Neoparasitidae species A-6: Species A-6 was found on pinned males of *Neivamyrmex harrisi* which had been in the Snow Entomological Museum, University of Kansas, for more than 20 years. These mites remained on the dry specimens in spite of shipping the males to Brasil for determination and in spite of repeated handling. This mite is phoretic rather than parasitic on the males. All the specimens were found clinging to the hairs of the propodeum by means of chelicerae, palpi, or both, and clearly were not using any legs to hold onto the ants. A total of 11 mites was found on 111 male ants from Arizona, Texas and México. Probably all these ants had been taken at lights. No Neoparasitidae were found on more than 200 males of other species of *Neivamyrmex* taken primarily in the same geographical area.

Sphaeroseius Berlese: The genus *Sphaeroseius* has been placed in family Laelaptidae by Berlese (1904a: 243) and Sellnick (1925: 5) and in the Neoparasitidae by Radford (1950: 12) and Baker and Wharton (1952: 73). The following species have been described: *ecitonis* (Wasmann, 1900: 256), *comes* (Moniez, 1895: 203), and *praedatoris* Sellnick (1925: 5-8). *S. ecitonis* was found "in a column of *Eciton coecum*" [= *L. coecus*] [translation] and not with *E. schmitti* or *E. coccum* as stated by Berlese (1904b: 434, 456). *S. comes* was found "in abundance in a column" [translation] of *L. praedator* (Moniez, 1895: 205) with no mention that it was *on* the ants as stated by Sellnick (1925: 8). *S. praedatoris* was found on *L. praedator* according to Sellnick (1925: 9). All three species were described from ants taken in Brasil. No specimens which at all resemble this genus were found in Panamá. However, in Reichensperger's collection I found two specimens which appear to be *Sphaeroseius*; these were taken with *L. coecus* in Costa Rica. On the basis of the above meager evidence, this genus appears to be restricted to *Labidus praedator* and *coecus*. The statements in the literature leave doubts as to whether this genus has been seen running with the ants or riding on them. The unusually long legs may be an adaptation for running during the emigrations or for clinging to the ants.

Larvimimidae: Larvimima Rettenmeyer

Four species of very unusual mites which mimic ant larvae (figures 21 to 25) are here placed in a new genus, *Larvimima*, in a new family Larvimimidae. These mesostigmatid mites are so highly specialized for living within ant colonies that their affinities to other Parasitoidea are obscure. However, they appear to be most closely related to the Laelaptidae and Neoparasitidae. The four species lack sclerotized dorsal plates, and the few ventral plates are reduced, weakly sclerotized, and highly modified from those of free-living Parasitoidea. The fixed digit of the female chelicera is blunt and only about one-fourth the length of the movable digit.

All four species show a remarkable resemblance to the larvae of the ants. Several specimens were overlooked in sorting through samples of thousands of ant larvae. The first specimen was discovered when it was seen walking among some *Eciton* larvae. Since army ant larvae are incapable of any locomotion other than an inefficient squirming movement, this specimen was made conspicuous by its slow, straight walk.

The similarity to the ant larvae is based on several factors: (1) the elongate shape which is due to a tremendous elongation of the opisthosoma (the area posterior to the hind legs). The smallest specimens have an opisthosoma which is approximately equal in size to the prosoma (the entire region anterior to the hind legs). In most of the specimens the opisthosoma is the same approximate width but two to twelve times the length of the prosoma. (2) The body is almost as thick as it is wide, approaching the cylindrical form of the Eciton larvae but lacking the more narrow head region of the ant larvae. (3) It is entirely white except for the legs which are light yellow-brown. In preserved samples these mites are more opaque in appearance than the ant larvae. This contrast in opacity is not as apparent in the living mites and larvae. These mites also tend to absorb more color from the preserving fluid than the ant larvae. (If large numbers of adult ants are preserved in a relatively small amount of alcohol, this alcohol becomes brown, and mites and ant larvae absorb some of this color.) (4) The opisthosoma (but not the prosoma) has indentations or annulations somewhat like the intersegmental constrictions of the ant larvae. One species has the opisthosoma divided into about ten "segments." In comparison, the ant larvae have 12 thoracic and abdominal segments. The other three species of Larvimima have the opisthosoma divided into three distinct segments (cf. figures 23 and 25). The large posterior segment showed a slight division into two segments in the living specimen (figures 21 and 22). (5) Larvimima has a pile-like covering of body setae which are similar in density, length and thickness to the setae on the ant larvae. These setae are visible in figures 22 and 24. The smaller male mites have shorter setae similar to the smaller ant larvae. All the setae on the body of Larvimima are extremely similar. The usual three pairs of sternal setae typical of Mesostigmata cannot be distinguished from any of the other setae in the sternal region, and no sensory setae can be found on the body except for some on the appendages.

At the present time, before detailed descriptions of these mites have been made, one can best place these mites in one genus including four species. Some specimens have been kept in alcohol to preserve more closely their natural shape, and these can only be determined to genus. The species fall into two groups on the basis of their superficial body shape. In the first group of three species the opisthosoma is divided into two narrow anterior annulations with the rest of the opisthosoma showing no distinct indentations (figures 21, 22, 24 and 25). In the second group, which includes a single species, the opisthosoma is rather evenly divided by annulations into pseudosegments for its entire length (figure 23).

The swollen appearance of the opisthosoma and the lack of a clear female genital opening suggest that Larvimima may produce a large number of eggs which may be released when the female ruptures. However, the only female in which any immature stages were found contained only a single large egg. No other immature specimens have been found. The four smallest individuals shown in figure 25 are males belonging to the same species as the largest two.

Only 44 specimens of Larvimima were taken, indicating that this is one of the rarer mites found in army ant colonies. Although it is possible that a few specimens may have been missed in sorting through large samples of larvae, this mite normally must not be abundant in the colonies. Since one would expect this mite to be found only with the ant larvae, the number of mites should be compared not with the total number of workers but with the total number of larvae taken. The latter ratio would be about 24:128,013 or 1:5,334 based on the specimens from Barro Colorado Island. The highest incidence of this mite (1:614) was found in a colony of *E. hamatum*, E-211, where five mites were taken. The lowest incidence (1:41,809) was found in a colony of *E. burchelli*, '55 B-IV-N.

The degree of host specificity is uncertain because of the few mites which have been determined. However, three species have been found with a single host, *hamatum*, on Barro Colorado Island, and one of these was also found with *hamatum* from Darien Province, Panamá. The single mounted specimen from *burchelli* is a distinct species. The only other host for the genus *Larvimima* is *E. mexicanum*. Females are known for all four species, and the male for only one. No immature stages have been found except for an egg within a female.

Out of the 44 specimens of *Larvimima* which have been found, only one was seen alive in Panamá. This specimen (2101) was used for a series of tests with *Eciton* larvae and adults from colony E-211 in which the mite was found. In laboratory nests, army ant workers will usually pick up scattered larvae from their colony and pile them in one area of the nest. Workers were also observed to pick up the *Larvimima*, either alone or simultaneously with one or two *Eciton* larvae, and place it with the ant larvae. The mite showed no sign of injury after repeated moving by the ants. Aspirating workers carrying larvae on emigration columns also revealed that a few of these larvae were actually *Larvimima*.

The *Larvimima* specimen (2101) illustrated in figures 21, 22 and 24 was quite active when placed among the *Eciton* larvae. In spite of its huge opisthosoma, it could climb over the larvae and walk on the smooth paper floor of the nest. However, it would seem highly unlikely that it would be able to run along a typical emigration route of 75 to 300 meters, and thus, it must be dependent on the ants for transportation. The *Larvimima* usually stayed on the *Eciton* larvae where it moved its palpi (and chelicerae?) over most of the surfaces of the larvae. It may have been feeding on secretions or food particles. It was never seen to pierce the body wall of the larvae and never held tightly to a larva or any other substrate when it was moved by an ant or my forceps. When worker ants were standing among the larvae, the *Larvimima* continued walking on the larvae and showed no reactions toward the adults. The worker ants and larvae showed no attraction to nor irritation by the mite.

Larvimima species 1: This largest species of *Larvimima* is over two millimeters long. Only a single specimen (2194) found with *hamatum* has been mounted, but additional specimens probably are included among the mites in alcohol. The dorsal and ventral setae on species 1 are longer than in the smaller species of *Larvimima*. These longer setae contribute to the resemblance of the mites to ant larvae of corresponding size.

Larvimima species 2: A series of 19 specimens of *Larvimima* were found in a sample of E. hamatum taken by Dr. T. C. Schneirla from colony '48 H-D at the Pirre River, Darien Province, Panamá. Probably these all belong to species 2, but only nine specimens have been mounted. Part of this series is shown in figure 25a together with the ant larvae with which they were found. The ant larvae and eggs are stippled in figure 25b. Species 2 was also taken with *hamatum* on Barro Colorado Island.

Larvimima species 3: Only a single specimen has been mounted from a sample of *E. burchelli*, and this mite belongs to a third species. Only three specimens of *Larvimima* have been taken with this host even though more than three times as many larvae (98,074) have been examined from *burchelli* than from all other hosts combined. *Larvimima* must be much more rare with *burchelli* than with *hamatum* in Panamá, or else the occurrence of the mites is extremely sporadic in the colonies.

Larvimima species 4: Species 4 is represented only by the single unmounted specimen taken with *hamatum* larvae shown in figure 23. The unusually elongate shape and the arrangement of the coxae and ventral plates clearly indicate that it is a distinct species.

Laelaptidae

A few species of adult Laelaptidae have been found in the ant samples. In addition, there were a few nymphs of Parasitoidea which probably are laelaptids. However, only one genus of Hypoaspidinae, *Laelaspis* Berlese (1903), has been found repeatedly on several species of ants. At least some of the species of *Laelaspis* must be considered myrmecophiles. All the other laelaptids were found in smaller numbers and probably none of them is an inquiline.

Laelaspis Berlese: The genus *Laelaspis* Berlese (1903) was based on mites found with ants from Europe. The genus is close to other Hypoaspidinae which are commonly found with ants and other insects. The species from army ants are different from those described from Europe by Berlese. No species of *Laelaspis* from Central or South America was found in an incomplete survey of the mite literature. Among the ten species found on Ecitonini, there is considerable variation, especially in the chelicerae and ventral plates. A thorough revision of the related genera would be necessary to determine whether these species from army ants should be placed in Laelaspis or segregated into two or three genera.

Laelaspis may be a parasite of the army ants, but it is more likely a scavenger in the nests. None of the mites was ever seen near the mouthparts of workers or where the mites would have been able to puncture the ants for feeding. The only time Laelaspis was seen on workers it was riding on the upper side of the thorax of larger workers of Nomamyrmex esenbecki. Since two species were found to be common with this species of doryline, I am not certain whether one or both species was seen. Laelaspis species 8 was found by Mr. Earle A. Cross on the external genitalia of males of Labidus coecus taken at a light in Texas and preserved in alcohol. This series included nymphs, males and females. No other specimens of Laelaspis have been found on male Ecitonini.

Dr. Preston E. Hunter (personal communication) has found Laelaspis in leaf litter in Georgia where the mites may or may not have been associated with ants. He also has been successful in rearing one species, Laelaspis vitzthumi (Womersly), on freshly killed flies. If dead insects are the usual food of the genus, one might expect to find Laelaspis in the refuse deposits of the army ants. However, in the refuse deposits of E. burchelli, which were the only ones thoroughly sampled, no Laelaspis was found.

Each species of Laelaspis was found on a single species of host except species 5 which was found on two hosts. The apparent high degree of host specificity supports the belief that all the Laelaspis from army ants are new species. However, all species, except species 6 and 7, are represented by only a few specimens. In addition to seven species from

Barro Colorado Island, three were found with army ants taken in Texas or British Guiana.

The only time a large number of Laelaspis was taken was with Nomamyrmex esenbecki. In colony E-164 a total of 247 Laelaspis was taken with 2,739 workers, a ratio of 1:11 (or a ratio of 1:14 based on all N. esenbecki collected). Such high infestations or "epidemics" are rare since 19 samples of Nomamyrmex from 16 colonies had a total of two specimens of Laelaspis. This is at a ratio of 1:408 ants. The ratios for all other species of Laelaspis are smaller than 1:1,000 based on the total ants examined for each species. (Species 4 was taken with E. mexicanum in the proportion of 1:9, but only in a single sample of 17 ants.) A summary of the number of mites collected for each host is given in table 10.

Perhaps wide fluctuations in the populations of these mites are possible within an individual colony. However, it does not appear that regular fluctuations are present in all colonies, nor is it likely that such fluctuations are correlated with the nomadic-statary cycle of the ecitonines. Enough samples of hamatum and burchelli have been examined that if there were a regular peak in the Laelaspis population at any time in the nomadic-statary cycle, it should have been evident in at least a few of the samples. In this connection it should be pointed out that the Nomamyrmex colony E-164 was sampled at the time of an emigration when there were many callows, and the workers were carrying larvae. Similar samples of the more common army ants have been taken frequently at the beginnings of nomadic phases without finding large numbers of Laelaspis. Colony E-178, E. mexicanum, was sampled from raid columns coming from the same hole in the ground on two successive days which may indicate that the colony was in a statary phase.

Laelaspis is not only unusual in its sporadic occurrence, but it differs from most other myrmecophiles associated with the Ecitonini in that males, females and nymphs are all relatively common. There does not seem to be any correlation in size between the species of mite and the species of host. The genus does not seem to show any adaptations for myrmecophily other than possibly longer setae and a more flattened body than is found in many free-living Laelaptidae.

Laelaspis species 1: This species was found in five colonies of *L. praedator*. It was found more consistently with its host than any other *Laelaspis*. However, it was still a rare mite. Three of these collections are based on single adults, and one is based on one adult and one nymph. The ratio of mites to ants is 1:1,626.

Laelaspis species 2: Only a single specimen of *Laelaspis* sp. 2 was found even though its host is *burchelli*, the host from which we have examined the largest number of samples and workers.

Laelaspis species 3: Two nymphs, five males and five females of this species were found, all in one colony of *E. hamatum*. *Laelaspis* species 3, like species 2, appears to be either a very rare myrmecophile or it is unevenly distributed among the colonies of its host species.

Laelaspis species 4: *E. mexicanum* is the host for species 4 which is represented by only two males. These two mites were found with a total of 17 workers from a single colony, indicating that this colony may have had a heavy infestation by this mite.

Laelaspis species 5: This species is the only Laelaspis which has been found with two hosts (Eciton burchelli and Neivamyrmex gibbatus). In view of the widely separated taxonomic position of these two hosts, this laelaptid throws doubt on the degree of host specificity found in Laelaspis. Unfortunately only two specimens were taken, and it is therefore impossible to determine whether the slight differences between the specimens indicate specific distinction.

Laelaspis species 6: Eight males and 27 females of species 6 have been determined among the Laelaspis taken with ants from an emigration of colony E-164 (Nomamyrmex esenbecki). One additional female was found in a second colony, but no others were found in samples from 16 additional colonies. An additional 175 Laelaspis were taken in sample 1826 from colony E-164, but these were not mounted on slides. These unmounted specimens must include both species 6 and species 7 found in the same sample. In sample 1826 the number of specimens of species 6 (3♂, 13♀) appears to be approximately equal to the number of species 7 (3♂, 10♀). In addition, six nymphs were mounted from this same sample; these have not been referred to either of the two species. Based on the proportions of the mounted series, the unmounted specimens are estimated as 43 females, 21 males and 21 nymphs of species 6. A few specimens of either species 6 or 7 were seen on the thoraces of larger workers in the emigration column of colony E-164. This case is the only time Laelaspis was seen on any living ants.

Laelaspis species 7: The number of mounted Laelaspis from colony E-164 includes a total of five males and 26 females of species 7. In addition to these, approximately 21 males and 43 females have been kept in alcohol. (The numbers of these were estimated as discussed under species 6.) In addition, about three mounted nymphs and 21 unmounted nymphs, which probably belong to this species, were taken at the same time as the adults. This species may have been the *Laelaspis* seen riding on the dorsum of the thoraces of several larger workers during the emigration of colony E-164.

Laelaspis species 8: This species is known only from a series found on males of *Labidus coecus* taken at Palmetto State Park, Gonzales County, Texas on 5 April 1954 by a University of Kansas Texas Expedition. These *Laelaspis* were found on the external genitalia of males which flew to lights. This species and the Neoparasitidae species 5 and 6 are the only mites which have been found on males after they have flown from their parent colony.

Laelaspis species 9 and 10: One male and one female of species 9 and one male of species 10 were found with a sample of *E. burchelli cupiens* taken in British Guiana by Dr. Neal A. Weber. With this subspecies of *burchelli* were found several other species of mites which are closely related but distinct from those found with the subspecies *E. b. foreli* of Barro Colorado Island.

Uropodidae

The cohort Uropodina includes many described species which have been found with ants. Most of the species belong to the family Uropodidae (in the strict sense of Baker and Wharton [1952]). Although a few specimens of uropodids have been found with army ants and even attached to these ants, they are much more rare than the three families, Circocyllibanidae, Planodiscidae, and Coxequesomidae. These three families are apparently more highly specialized forms of uropodines which probably have evolved from the Uropodidae. The Planodiscidae seem to be a more distinct and homogeneous group than the other two families, on the basis of the shape of the dorsal and ventral plates and the pattern of setae. However, there are several undescribed species which seem to be intermediate between the families Circocyllibanidae and Coxequesomidae.

Two described species have been found on army ants, and my material includes several other undetermined species of Uropodidae. None of these species shows any obvious morphological specializations for myrmecophily. Like some of the species of Uropodidae found on nondoryline ants, several species of Uropodidae have been found on strigils of army ant workers. The uropodids hold onto the tips of the strigils by a front leg, one palpus, or both. The uropodids found in this position may feed on substances cleaned off the ants' bodies when the ants clean themselves using the strigils.

Uropodidae are abundant in litter on the forest floor and in the refuse deposits of E. burchelli. Some of these mites may get on the ants possibly by accident, but these probably would not be found clinging to particular parts of the ants such as the strigils. Uropodidae were also found on nondoryline ants from Barro Colorado Island, but these are different species than those from the Ecitonini. The large number of morphologically similar species of Uropodidae which have been described makes specific determination impractical at the present time.

Uroplitella brasiliensis Sellnick: Uroplitella brasiliensis Sellnick (1926: 33) is based on a single female taken with Eciton quadriglume in Brasil. There is no indication that the mite was actually found on an ant. Since Sellnick reported that other species described in the same paper were actually found on an ant, this mite may have been free in the vial.

Marginura adhaerens Sellnick: This species was also based on a single female, but no type locality or host other than "*Eciton*" were given by Sellnick (1926: 39). Presumably the mite came from southern Brasil where the other specimens he described were collected. No reliable guess can be made as to the species of Ecitonini involved. *M. adhaerens* was found attached to the strigil of an army ant, probably either a species of *Eciton* or *Labidus*.

Planodiscidae

This family of Uropodina is based on *Planodiscus sqamatim* Sellnick (1926: 44), and no additional species have been described. Ten new species have been found in this survey. All the species of Planodiscidae are at least one and one-half times as long as wide and have one main ventral plate including the fused sternal and ventral plates. In addition, there is a pair of ventral marginal plates which extend at least half the distance from the posterior end of the sterno-ventral plate to the fourth coxae. The size and proportions of the ventral plates are the most conspicuous specific characters in the family.

The species of Planodiscidae have been tentatively divided into two groups of species or subgenera based on the position of the metapodal carina. In subgenus A the metapodal carina extends along the inner margin of the metapodal plate, whereas in subgenus B, the metapodal carina extends approximately through the center of the plate. This character can be easily seen on specimens in alcohol using 40X magnification.

All species of Planodiscidae are known from the genus *Eciton* except for species B-10 which is based on one specimen found with *Neivamyrmex*. This specimen was found in a sample of about 250 workers from a colony of *Neivamyrmex legionis*. Over 20,000 other specimens of *Neivamyrmex* spp. have been examined without finding additional Planodiscidae. Furthermore, since over 1,500 specimens of planodiscids have been found exclusively with *Eciton*, the one record from *Neivamyrmex* is most unusual. A summary of the host records is given in table 11.

Unlike many of the other mites, these mites are not restricted to the major workers or even the submajors. They were found primarily on the larger intermediates but also were seen on small intermediates, though never on the smallest individuals or minims.

Species A-2, B-1, B-5 and B-7 were seen riding on the undersurfaces of tibiae. In view of the elongate form and the shape of the dorsum and venter, it can be expected that every species has the same habit. The anterior end of the dorsum is slightly prolonged to form a rounded point. On each side of this blunt point there are weak emarginations. When a planodiscid is on the underside of the tibia of an ant, and the ant bends its leg strongly, the dorsal prolongation fits between the two ventrolateral ridges on the underside of the ant's femur. The ventral plate is somewhat concave and in most species it has an elongate groove that fits against the tibia of the ant. In several species this groove is deepened by a longitudinal ridge along each side slightly medial to the bases of coxae II to IV.

The planodiscids found with *hamatum* and *burchelli* were frequently seen on larvae although they usually did not leave workers which were placed in laboratory nests with larvae. Probably these mites feed on the larvae, but there is no certain evidence for this. The planodiscids were never found on or inside the ant cocoons. It is also not certain if the planodiscids feed on the adult ants. It seems likely that they may insert their chelicerae into the membrane on the underside of the joint between femur and tibia. The chelicerae are long enough for this if they can be extended for most of their length. However, those planodiscids which were examined with a microscope did not have their chelicerae inserted in this membrane when they were on the legs of living ants. On several occasions, planodiscids were observed to climb up on legs of workers. At these times, the workers either scraped the leg with the mite against another leg or rubbed the leg with the mite with another leg. These rubbing motions indicated that the mite was irritating the ant. In all cases the ant was unsuccessful in dislodging the mite. When one worker was touching the leg of another which had a planodiscid on it, the second worker made no attempt to bite or remove the mite. It is interesting that the workers appeared to be irritated by the planodiscids in view of the fact that the same species of ants paid no noticeable attention to the Circocyllibanidae. Mites of the latter family were more frequently seen walking on the workers. Even when climbing on the heads, antennae or legs of the ants, the *Circocylliba* spp. elicited no reaction from the workers.

Planodiscus squamatus Sellnick: The original spelling of the type species of *Planodiscus* is *sqamatim* Sellnick (1926: 44). It has been emended to *squamatim* by Radford (1950: 53) and to *squamatum* by Baker and Wharton (1952: 112). Sellnick selected this name apparently because the mites, or reticulations on the mites, look like scales. The name *sqamatim* is apparently a *lapsus calami* even though it appears several times with the original description (published in Brasil in German and Portuguese). The best procedure, for a name which has been used as infrequently as this one and possibly emended incorrectly, would be to emend the spelling to *Planodiscus squamatus* to agree with the Latin masculine ending.

The type series of this species was in the collection of Dr. M. Sellnick which was destroyed during World War II. Father T. Borgmeier has sent me two series of mites which appear to be *P. squamatus*, and one of these is from *E. quadriglume*, the host of the type. This series includes six males and one female. The second series was found with *burchelli* and includes seven males and two females. The sex ratio for all other species of planodiscids has been close to one male to two females, and no sample of any size has included such a large proportion of males. *P. squamatus* belongs in subgenus A in the tentative separation of the species used here.

Planodiscus species A-2: *Planodiscus* species A-2 was found with *E. burchelli*, but only about one-fifth as frequently as species B-1 on Barro Colorado Island. The rarer species was not found in samples from Trinidad and British Guiana, whereas species B-1 was taken at those localities. Since species A-3 and A-4 were found in the same samples from British Guiana as species B-1, it is possible that the former two replace species A-2 south of Panamá.

Planodiscus species A-3 and A-4: *Planodiscus* species A-3 and A-4 were found in a single large sample of *E. burchelli* cupiens (colony D-137) taken in British Guiana by Dr. Neal A. Weber. It is interesting that three species of *Planodiscus* were represented in this colony, and that species B-1, most common in Panamá, was the least common in this sample. Species A-3 and A-4 were approximately equal in abundance (species A-3: 30♂, 26♀; species A-4: 20♂, 25♀).

Planodiscus species A-6: Species A-6 was found on Barro Colorado Island with species B-7 in colonies of *E. mexicanum*. Only seven specimens of this species were taken in a total of three colonies.

Planodiscus species A-9: Species A-9 is represented only by a single male taken with *E. vagans* on Barro Colorado Island.

Planodiscus species B-1: By far the most common species of *Planodiscus* was species B-1 which was found with three subspecies of *Eciton burchelli*, *foreli*, *cupiens* and *urichi*, from Panamá, British Guiana and Trinidad respectively. It also was taken with *E. vagans* on Barro Colorado Island but appears to be rare with that species since only two specimens were taken (a ratio of 1:6,883). A total of 950 specimens were found with *burchelli* from all localities (a ratio of 1:648).

Planodiscus species B-5: Species B-5 was found with both *hamatum* and *vagans*. Although it is not common with *vagans* (ratio 1:1,530), it was found in five colonies out of 13. In samples of *hamatum*, 165 specimens were found, a ratio of 1:392. This species was also found in a sample of *hamatum* from Darien, Panamá, the only locality, other than Barro Colorado Island, from which a large sample of *hamatum* has been examined.

Planodiscus species B-7: Species B-7 is narrower and longer than any of the other species of *Planodiscus*. However, it is found in the same position on the tibiae of the ants as the much broader species of *Planodiscus* (species B-1, A-2 and B-5). Species B-7 is of interest because it has been found on three species of hosts: *hamatum*, *dulcius* and *mexicanum*. The total of 54 specimens shows this host distribution: *hamatum*, 35 (1:1,848); *dulcius*, 4 (1:1,514); and *mexicanum*, 15 (1:345). Since the specimens from *mexicanum* were taken in samples from five colonies the much higher incidence with this host is not due to an unusually high population in one colony.

Planodiscus species B-8: The three known specimens of this species were found in a sample of *E. vagans angustatum* taken in Chiapas, México by Dr. T. C. Schneirla. This is an additional case of two subspecies of army ants having closely related but distinct species of mites found with them. *Planodiscus* species B-1, B-5 and A-9 were found with *E. vagans mutatum* from Barro Colorado Island. Species B-8 was the only *Plandiscus* found with about 2,000 workers of *E. vagans angustatum* from southern México.

Planodiscus species B-10: Species B-10 is the only planodiscid known from a genus other than *Eciton*. A single specimen of this elongate species was found in a sample of *Neivamyrmex legionis* taken by F. Plaumann in southern Brasil. Although approximately 60,000 workers and larvae of army ants from the genera *Labidus*, *Nomamyrmex* and *Neivamyrmex* have been examined, no other specimens of Planodiscidae were found with these hosts. The general shape of this species indicates that it is not closely related to the other species and perhaps it should be placed in a third subgenus.

Circocyllibanidae

The Circocyllibanidae differ from almost all other Uropodina by having a highly convex dorsum which extends beyond the edges of the venter and entirely covers legs II to IV. The claws and sometimes the distal segments of the legs may be extended beyond the edge of the dorsum when the mite walks. In most preserved specimens, the legs are pulled into large depressions. The ventral plates are highly variable. In *camerata*, the type species of the genus *Circocylliba* and the only described species in the family, there is a large ventral plate, a small anal plate, and a pair of small posterior marginal plates. These plates and also the metapodal plate show varying degrees of coalescence in other species. The extent of this fusion has been the main basis for separating the new species of circocyllibanids into tentative genera.

The circocyllibanids are about one-fourth as common as the planodiscids; however, they are found on *Eciton*, *Labidus* and possibly *Neivamyrmex* (see *Discopoma* at end of Circocyllibanidae). A summary of the host records is given in table 11. Most of the species were found on one or two hosts, but *Circocylliba* sp. 1 was taken with five species of *Eciton*. Each species of mite appears to have one or several preferred positions where it rides on the ants, as described below. All the species which were seen on the adult ants seem to spend hours going over the surfaces of the ants with their palpi (and chelicerae?). The large amount of time spent in this activity suggests that they are feeding on particles or secretions on the body surface. Several species also seem to feed on the surfaces of ant larvae and perhaps puncture the body wall. If the mites feed on surface secretions, this may be important for acquiring the colony odor.

Circocylliba camerata Sellnick: C. camerata was described by Sellnick (1926: 40-43) from specimens collected with Eciton quadriglume and burchelli. Unfortunately, the two series of mites could not be distinguished by Sellnick except by size (and host), and he considered them one species. His drawings and description do not give any indication as to whether they were based on one or both sizes of mites. There were apparently no specimens intermediate in size between the two groups measured by Sellnick. The two groups differ by approximately 200 microns in both length and width. The type series was destroyed during World War II, but the size and host differences are strong evidence that it included two species.

Circocylliba species 1: This species was both the most abundant circocyllibanid in any colony and was found with the greatest number of hosts. Judging from the size, shape and body setae, species 1 is closest to the Uropodidae. It has been found with burchelli, hamatum, dulcius, vagans and mexicanum. With vagans, species 1 appears to be rare (only a single specimen was found), but with all the other hosts it consistently was found in small numbers. Since all the records for species 1 are from Barro Colorado Island or Darien, Panamá, this species may have a limited geographical range. No specimens of species 1 were found in the following samples: burchelli urichi (Trinidad), burchelli cupiens (British Guiana), hamatum (México) and vagans angustatum (México). The smallest of these samples was about 2,000 workers, whereas the other three samples were 6,000 to 10,000 workers, and all four samples included other species of circocyllibanids.

Circocylliba species 1 appears to prefer three positions on the worker ants. These are dorsolaterally on the head, middorsally over the highest part of the alinotum, and middorsally on the gaster (usually on the first tergum). These are positions where the mite seems to fit best, *i.e.*, the convex curvature of the ant is similar to the concave curvature of the mite, and the area of the ant is large enough for the entire edge of the mite's dorsum to come in contact with the ant's body. A mite on a gaster is shown in figure 16. Species 1 was seen to walk over any part of the dorsal and lateral surfaces of the workers, but it was not seen on the ventral surfaces. One would expect that it would be scraped on the ground if it rode on the ventral surface of the gaster, and the coxae of the workers do not appear to have large enough surfaces for the Circocyllibanidae. None of the circocyllibanids rides in symmetrical or balanced positions on the ants as has been reported for other mites with nondoryline ants.

Cirçocylliba was frequently seen on the ant larvae, and in laboratory nests where unusually high populations of these mites were kept for study, the mites covered about one half of the surface of a larva. Three specimens of this species can be seen on the larva in figure 16. In this figure, one can see that the dorsum of each mite fits tightly against the surface of the larva and not even the tips of the legs are visible beyond the edge of the dorsum. The entire gnathosoma is also hidden under the dorsum, making it impossible to observe how the mite feeds. The mites are difficult to remove from the larvae which may be an adaptation for preventing removal and attack by the workers. However, no workers were ever seen to attack any of the mites from any family, and no apparent irritation is caused by the circocyllibanids. Perhaps the evenly distributed covering of setae on the dorsum of the Circocyllibanidae, which is similar in appearance to that on the surfaces of the ants or their larvae, makes the mite more difficult for the ants to distinguish. When large larvae were present in a colony, a high percentage of the individuals of species 1 were found on the larvae. When the larvae spun cocoons the mites shifted back to the adult ants. One specimen was found inside a cocoon of an intermediate _Eciton_ worker where it presumably was trapped accidentally.

Circocylliba _species_ _2_: This species was also found with _E_. _burchelli_. It can be easily distinguished from species 1 by its larger size and longer dorsal setae. There are other differences which can be seen only after the specimens have been mounted on slides. A few specimens were found which had lost most of the longer dorsal setae, and therefore this character may not always be reliable. This loss of dorsal setae is probably caused by the dorsum of the mite being rubbed against ants or other objects. There is no evidence that the ants attack the mites and thus pull or break the setae off.

Seven specimens of species 2 were taken with _E_. _mexicanum_ in addition to 54 from _burchelli_. No other myrmecophilous mite was found with this host combination (not including species found with other hosts in addition to these two). The specimens from _mexicanum_ were found in four of five colonies from which over 100 ants were examined. The specimens with _burchelli_ were found in only six of 13 colonies from which samples of over 100 ants were examined. This would suggest that species 2 is much more common with _mexicanum_ than with _burchelli_. The ratios based on mites per ants support this conclusion (1:653 for mexicanum, 1:9,213 for burchelli).

Like species 5 shown in figures 17 and 18, species 2 rides on the inner concave surfaces of the mandibles of major workers. It was found in this position on mexicanum at least four times. In spite of much more extensive observations of burchelli, it was seen only once on a mandible of a burchelli major. The ratios of species 2 with the majors of the two hosts are about the same (1:35 for mexicanum, 1:48 for burchelli).

Circocylliba species 3: Species 3 is known only from the sample of E. burchelli cupiens (colony D-137) taken in British Guiana. It is of interest primarily because it is very close to species 1 which is common with E. burchelli foreli from Barro Colorado Island.

Circocylliba species 4: Species 4 has both long dorsal setae and long setae on the entire surface of the ventral plate. The ventral plate is also strongly reticulate unlike any other Circocylliba. Species 4 was found on the mandibles of both dulcius and vagans (see figures 17 and 18). The workers of these two species of Eciton are practically identical in size and morphology.

Mites in this position on the mandibles of the major workers would appear to be susceptible to crushing when the major bites any object. However, many times when a major worker bites, only the tips of the mandibles come in contact with the object bitten. In these cases the mite can stay on the inner surface without being injured. If anything touches the dorsal setae or dorsum of the mite, the Circocylliba shifts temporarily to the outer surface of the mandible.

Species 4 is the largest of the species of *Circocylliba* (about 1.5 mm. in length), and it is quite conspicuous when an ant with one or two of these mites is seen from the front. The mites can be seen on emigration columns at night even in dim red light, and one or two majors were seen with a *Circocylliba* on both mandibles. However, in lateral view the mite is difficult to see because this species is more flattened than the other *Circocylliba*, and it stays in the concave area of the mandible. In this position it is not susceptible to being knocked off if the major collides with another ant or scrapes against some object. Since the majors run more slowly and more frequently reverse their direction in an emigration column, other workers collide with them. In the laboratory, several specimens were removed from the major workers, but each time the mites climbed up the legs and went to their habitual positions on the mandibles. At no time did the majors make any attempt to scrape the mites off their bodies even when the mites were climbing over their eyes, antennae or mouthparts.

Circocyllibanidae species A-1: This species was found on a queen of *hamatum* taken in southern México by Dr. T. C. Schneirla. It differs greatly from all the species of *Circocylliba* found on *Eciton* and has been tentatively assigned to a new genus. The most obvious differences from *Circocylliba* are: the dorsum is less highly arched, the anal plate is fused to the ventral plate, and the posterior marginal plates are almost fused to the ventral plates. No specimens of Circocyllibanidae were found on about 30 living *Eciton* queens which were examined from Barro Colorado Island. In the laboratory, queens of all five common species of *Eciton* were observed with the various species of circocyllibanids. As far as could be determined with these few trials, the mites showed no preference for the queen compared with workers or larvae. Species A-1 may be unusual if it shows such a preference for a queen. Unfortunately the exact number of mites which were on this queen is not known, but apparently it was more than seven. Nothing is known about other circocyllibanids which may have been present in the same colony as this queen.

Circocyllibanidae species B-1: Three species of Circocyllibanidae have been grouped into a second new genus on the basis of the greater coalescence of the ventral plates. In addition, these three species are all found on *Labidus* with which no *Circocylliba s. str*. has been found. The most conspicuous generic characters are the unusually long dorsal setae and the fusion of the ventral, anal and posterior marginal plates. Species B-1 has only been found with *L. praedator* from Barro Colorado Island. About 600 specimens of *praedator* have been examined from other localities without finding any species of Circocyllibanidae. None of the circocyllibanids from *Labidus* have been seen on the living ants.

Circocyllibanidae species B-2: This species is clearly close to species B-1 but differs in several prominent characters, such as the proportions of the leg segments and the shape of the ventral plates. It was found only with *Labidus coecus*, was present in five out of six samples of over 100 ants, and was found with five out of seven colonies. Species B-2 was also among the most abundant of the circocyllibanids with a ratio of 1:141. (For comparison, species B-1 with *praedator* was found in samples from five out of 22 colonies at a ratio of 1:1,025.)

Circocyllibanidae species B-3: Species B-3 from British Guiana is clearly distinct from species B-1 and B-2 from Panamá but is closely related to those species and also was found with the same genus of ants. Only one male and one female of B-3 were found in a sample of *L. coecus*. Borgmeier (1955) was unable to separate *coecus* into subspecies even though it ranges from Texas to Argentina, a much larger range than *L. praedator* and several other species which he did divide into subspecies. Likewise the circocyllibanids found with *E. burchelli* and *L. praedator* from British Guiana are distinct species from those found in Panamá with the same species of host.

Circocyllibanidae species C-1: Although only a single female of this species was found, and it has not been mounted on a slide, it clearly is different from any other uropodine found with Ecitonini. In dorsal view, it is perfectly circular; in lateral view, the dorsum forms a low arch with bluntly rounded angles and a narrow vertical marginal area. In brief, the mite looks like a round pill with a weakly convex dorsum and a weakly concave venter. Species C-1 was taken with *L. coecus* on Barro Colorado Island.

Circocyllibanidae species D-1: Another species is tentatively placed in a genus which seems to be somewhat intermediate between the Circocyllibanidae and the Coxequesomidae. Unfortunately only a single female was found, and this has not been mounted. The general shape of the mite resembles that of a derby hat or a bonnet with a broad brim on all sides except the posterior margin. This broad "brim" is a continuation of the dorsum. The venter is no more concave than in many of the circocyllibanids, however the dorsum is more highly arched much as in the coxequesomids. It was found in a sample of *L. praedator* from Barro Colorado Island.

Discopoma, Cilliba, Cillibano and Thrichocylliba: *Discopoma hirticoma* (Berlese, 1904a: 246) appears to be closely related to the Circocyllibanidae. *D. hirticoma* was based on mites found on a queen of *Neivamyrmex nigrescens* in Texas by W. M. Wheeler. A figure showing 29 mites on this queen was published by Wheeler (1910: 258, 409) who also published poor copies of Berlese's figures of the mite. Berlese (1904b: 331-332) redescribed this mite and stated that the types are in the Wasmann collection. I could find no such type in that collection but did find a single male specimen labelled "*Cilliba* (*Discopoma*) sp." taken at "Austin, Texas, 16/6. 1900, b. *Eciton nigrescens* Cress. Wheeler n. 7." This mite was mounted on a card which made only a superficial examination possible. On the basis of this examination, the description by Berlese, and the host record, it is probable that *D. hirticoma* is a species of Circocyllibanidae. The type of this species may be in the Berlese collection.

The mite *Thrichocylliba comata* (Leonardi) (=*Discopoma*, =*Cillibano*?) was found with *Lasius*, *Camponotus* and *Myrmica* (Berlese, 1904b: 331), and it is impossible to tell how closely it may be related to the Circocyllibanidae. Perhaps all these mites belong with *Cilliba* in the Cillibidae, but without an extensive study of the Uropodina along with examination of many types, it is most convenient to refer mites of this type which are found with Neotropical Dorylinae to the family Circocyllibanidae.

Coxequesomidae

Although three species have been described in this family, the Coxequesomidae were by far the rarest of the families of Uropodines found with Ecitonini in Panamá. The fact that the Uropodidae and the Coxequesomidae are the only families of Uropodina which often remain attached to preserved army ants probably accounts for the greater number of described species in these families. One species of Coxequesomidae was seen riding on the mesonotum of a worker of *Labidus praedator*. All other species in this family which have been seen on ants, were seen on coxae or antennae. Because of the unusual morphology of these mites, probably most species are found on appendages. The venter is deeply concave with the edges of the dorsum extending far below the highest point of the venter. In dorsal view, one sees a much smaller area of the dorsal plate than one sees in a lateral view of the mite. Figure 20 shows the greatly enlarged lateral surface of an *Antennequesoma* sp. The dark outline along the lower right edge of the scape is actually the margin of the dorsum. In posterior view the mite appears as in figure 19. The lateral margins of the dorsum extend around the scape so that the mite is actually in contact with three surfaces of the scape. Every other species of Coxequesomidae has a similarly developed dorsum which appears to be of prime importance for holding the mite on the ant. It would seem that unless these mites have some mechanism for changing the shape of the dorsum, and thus "grasping" the appendage with it, they must be restricted to specific areas and sizes of ants.

Coxequesoma collegianorum Sellnick: Both the male and female of *Coxequesoma collegianorum* Sellnick (1926: 47-51) were described from mites found on the coxae of *E. quadriglume*. The original description does not give the number of mites found, and no additional specimens belonging to this species have been collected. The only species of *Eciton* with which any Coxequesomidae have been found is *quadriglume*, a species which does not extend as far north as Panamá.

Coxequesoma species 1: A total of 14 specimens of a new species of *Coxequesoma* were found free in samples from four colonies of *L. praedator*. The ratio of mites to workers is 1:1,743 which is the second highest found for any coxequesomid with the Panamanian Ecitonini. One specimen was seen riding on the center of the mesonotum of a worker of *L. praedator*.

Coxequesoma species 2: Only two females of *Coxequesoma* species 2 were found in a single colony of *praedator*. The ratio to all workers of *praedator* is 1:12,199.

Coxequesomidae species A-1: The elongate shape of this species suggests that it is a new genus of Uropodina intermediate between the Planodiscidae and the Coxequesomidae. However, the anal and marginal ventral plates present in all known planodiscids are absent in this genus. Primarily for this reason, it is included here with the coxequesomids. Species A-1 also has a highly arched dorsum, but the lateral marginal areas of the dorsum extend below the level of the venter only for about the anterior third of the mite. As a result, when it is on its side (the normal position in alcohol) the mite has a somewhat hatchet-like appearance. For about the anterior third there is a broad lateral area of the dorsum visible, this narrows abruptly to form a long tail-like or handle-like opisthosoma. It is easy to overlook this mite because of the "assymmetrical" view one usually sees and the brown coloration which is similar to many fragments of the ant's insect booty. Although 30 specimens were found with *L. praedator*, none was seen on the ants. The elongate shape suggests that the mite probably rides on the legs or scapes of the ants. The ratio of mites to all *praedator* workers, 1:813, is the highest known for any species of coxequesomid.

Antennequesoma reichenspergeri Sellnick: The male and female of *Antennequesoma reichenspergeri* Sellnick (1926: 51-54) were found on both antennae and legs of *E. quadriglume* from Brasil. Unfortunately, the exact positions on the antennae and legs are unknown. Since many other Uropodina with Ecitonini have been seen only in a single position on an ant, it is noteworthy that this species was found on both legs and antennae. The type series of *A. reichenspergeri* was destroyed during World War II. However, Father T. Borgmeier has sent me a specimen found on the antenna of *quadriglume* taken at the type locality in 1925. It is quite likely that this specimen was taken at the same time as the type. No differences have been found between it and the description and figures by Sellnick. In addition, ten specimens taken in southern Brasil with no host record also appear to be *A. reichenspergeri*.

Antennequesoma lujai Sellnick: *A. lujai* Sellnick (1926: 54-55) was found on legs of *E. burchelli* from Minas Gerais, Brasil. Although the type series was destroyed during World War II, Dr. Reichensperger has loaned additional specimens to me taken at the same time as the type but not seen by Sellnick. One of these mites is still attached to the posterior dorsal surface of the right front femur of a small intermediate worker.

Coxequesomidae species B-1: Two species are believed to represent another genus of Coxequesomidae which has the dorsum more highly modified from the typical uropodine shape. The first of these, species B-1, is shown in figures 19 and 20, discussed above in the introduction to the family. In this genus, the dorsum is not only more highly arched than in the above species, but the midlateral parts of the dorsum are indented. The concave depression in the sides of the mite can be seen in the figures. A single specimen was found on the scape of a large worker of *Nomamyrmex esenbecki*. The mite matches the color of the ant perfectly and is so firmly attached that when this ant was first discovered, the coxequesomid was thought to be an abnormality of the antenna. Almost 3,500 specimens of *Nomamyrmex esenbecki* have been examined without finding any additional specimens of species B-1.

Coxequesomidae species B-2: The second species in coxequesomid genus B was found on the antenna of a small *Neivamyrmex* worker. The host was taken in México, and it is a small, new species close to *Neiv. opacithorax* (det. W. W. Kempf). This species of mite has a much deeper depression in each lateral area of the dorsum. In fact, the depressions are so deep that light passes through the two closely appressed surfaces of the dorsum at the center of the depressions. In lateral view, with light transmitted through the specimen, it appears that there is a hole in the mite. Perhaps a thorough study of the Coxequesomidae will show that both species in genus B should be included in *Coxequesoma* or *Antennequesoma*.

Antennophoridae: Antennophorus barbatus Wasmann

The single type specimen of *Antennophorus barbatus* Wasmann (1900) is the only antennophorid known from army ants. This record is surprising since no other trigynaspid Mesostigmata have been found with Ecitonini. In addition, most of the species of Antennophoridae known from ants have been found with *Lasius* in Europe and North America. The type of *barbatus* was found in a column of *Labidus praedator* in southern Brasil. It was not stated that the mite was actually seen on the army ants, and it is likely that the mite was booty of the ants or was an inquiline of some ant captured by *praedator*. Wasmann decided, on the basis of the long front legs without tarsal claws but with long setae at their tips, that this mite solicits food from the ants. Wasmann did not realize that all Trigynaspida and hundreds of other species of Mesostigmata have the same type of front legs, even though they are free-living species or are found with other insects.

I have seen the type in the Wasmann Collection (drawer 25) at Maastricht, Netherlands. It does not have any type label with it; however, it must be the type. The single specimen has a determination label in Wasmann's handwriting, and the locality and host agree with the ones published. Unfortunately, the mite is cemented on a card, and I could determine only that it is a female of the correct general shape and appearance of an antennophorid.

Scutacaridae

The family Scutacaridae is common on ants in many parts of the world, but no published records have been found of scutacarids from army ants. About 20 species were found with the Ecitonini during this study, and most, if not all of these are new species. On many occasions, scutacarids have been seen on worker ants. None has ever been seen on queens, males or larvae. On the worker ants these mites were invariably found on the ventral surfaces, and usually they were holding onto the carinae between the coxae. All the army ant species which have been examined have well-developed median longitudinal carinae on the sterna between all coxae. In addition, sometimes transverse carinae are fairly prominent. The scutacarids hold onto these carinae using their front legs, which in this family typically have larger tarsal claws than the other legs. A few specimens were under the front coxae of the workers.

Because of the small size of these mites, and the minute characters which separate species, it has not been feasible to determine them to species. None of the species can be sorted to species in alcohol though it might be possible to sort them partially after the mounted material has been adequately studied. About 600 specimens have been mounted, and over 300 specimens are still in alcohol.

All the Scutacaridae seen on the ants are considered to be phoretic. Only adult females were found.

Pyemotidae

The family Pyemotidae is the most abundant of all the families of mites found with the Ecitonini. Over 2,700 specimens were found and approximately 1,100 were mounted on slides. Pyemotids have been found with the four common genera, *Eciton*, *Labidus*, *Nomamyrmex* and *Neivamyrmex*, as well as with the African *Dorylus* (*Anomma*). Over 25 species have been found with the Neotropical Dorylinae, and a summary of the most common species with their host data is given in table 12. These are all new species, most of which belong to new genera. I am indebted to Mr. Earle A. Cross, Jr. for identifying the Pyemotidae. The names used are his manuscript names or numbers.

All the Pyemotidae which were seen on ants were found on workers. Most of these specimens were attached to the membrane behind the front coxae of all sizes of workers. A few were holding onto the ventral carinae between the coxae. The workers of all species of Ecitonini have an unusually large space behind the front coxae. Pyemotidae, and to a lesser extent, Scutacaridae, are found in this space. Each pyemotid appears to be attached by its gnathosoma and presumably feeds through the membrane at the bases of the coxae. The presence of three or four mites on one ant makes no noticeable difference in the ant's running. The mites usually cannot be seen on the workers without lifting the legs unless the mites are not attached. In alcohol, many of the mites no longer are attached, but remain partially under the coxae. Since it is too time-consuming to pull the legs of each worker forward to examine the coxal cavity for mites, this was done only for a few hundred workers of each species of host. Because many of these mites stay attached where they could not be seen in our sorting, and because of their small size, many specimens of Pyemotidae must have been overlooked.

Since so many species were found with no detailed information on any of them, the Pyemotidae will not be discussed here by individual species. Table 12 gives the total number of determined specimens of most species of pyemotids and the number of colonies of the hosts with which each mite was found. Species which were found only a few times are not given individually but are summed under "Species other than above." The row labelled "Species not determined" gives the totals of specimens still in alcohol. Over 13 species are not included in this table. However, all of these species are represented by less than seven specimens each. These specimens belong to the genera, *Siteroptes* Amerling, *Parapygmephorus* Cross, and *Glyphidomastax* Cross. The three most common genera given in table 12 are discussed below.

Acinogaster *Cross*: *Acinogaster* sp. 2 was found in a sample of *Dorylus* (*Anomma*) ?*nigricans* taken in Angola. This is the only clear case in which the same genus of myrmecophile has been found with Dorylinae from both the Eastern and Western Hemispheres. (The only possible exceptions to this statement may be one or a few genera of Staphylinidae close to *Zyras* or *Myrmedonia*. Poor knowledge of the generic limits of these Staphylinidae, combined with the presently impossible task of determining the more generalized species prohibit any accurate statements on the host relationships of these beetles.)

Acinogaster *marianae* is of interest because it was found with both *E*. *burchelli* and *hamatum* but not with any other species of Ecitonini. These two hosts have been considered to be closely related and have a number of inquilines in common. *A*. *marianae* was found in Panamá, Trinidad and British Guiana with the three different subspecies of *burchelli*. *Acinogaster* sp. 3 shows an unexpected host distribution, being found with *E*. *dulcius*, *Labidus* spp., *Nomamyrmex* spp. and *Neivamyrmex* spp. It may be lacking from the two most common species of *Eciton* because of competition from *A*. *marianae*, or its presence may be connected with the more subterranean habits of its hosts. Species 20 is more strange, since it is found with all the common Ecitonini in Panamá with the exception of *hamatum*. It also was found in British Guiana with *E*. *burchelli* *cupiens*.

E. hamatum was sampled so frequently that this lack of species 20 is highly significant. *Acinogaster* spp. 3 and 20 were found in both Panamá and Brasil. However, they were not found in Kansas with *Neivamyrmex*. Here only species 30 was found. Also species 5 was found only with *Neiv. legionis* in Southern Brasil. However, these data are only adequate to show that the last two species are not apt to be found in Panamá. *A. marianae* is the only pyemotid which was found also in a gravid condition (see figure 26a). None of these gravid mites, which look similar to ant larvae, were seen alive.

Myrmecodispus *Cross*: The genus *Myrmecodispus* Cross is based on the species *dorylinus* which was found in five colonies of *E. vagans*. It also was found in one colony of *E. burchelli*. In view of the large number of colonies of *burchelli* which were sampled, this species must be rare with this host. *M. dorylinus* was not found with *E. dulcius*, the species of ant considered to be most closely related to *vagans*. However, *Myrmecodispus* sp. 1 was found only with both *dulcius* and *vagans*. Three other species of *Myrmecodispus* were taken with ants from single colonies of *Nomamyrmex*. These data show that the genus *Myrmecodispus* is more rare and probably more host specific than *Acinogaster*.

Perperipes *Cross*: The genus *Perperipes* was found less frequently than the two genera of Pyemotidae discussed above. One species, *ornithocephala*, was found only with *hamatum*, and species 1 was found only with *burchelli*. A single specimen of *Perperipes* sp. 2 was found with *Nomamyrmex* *esenbecki*. The latter record indicates that the suggested preference for the closely related hosts, *burchelli* and *hamatum*, is not absolute.

Ereynetidae

There is some evidence that the family Ereynetidae includes myrmecophilous species. Almost 300 specimens of this family of mites have been found in samples from 17 colonies of Ecitonini, but none of these mites has ever been seen on the ants. Members of this family have been found with *burchelli*, *hamatum*, *dulcius*, *vagans*, *mexicanum*, *praedator*, *esenbecki* and *gibbatus*. *Ereynetes* sp. (det. G. W. Wharton) has been seen by Weber (1956: 154) on workers of the fungus-growing ant, *Trachymyrmex septentrionalis*, in laboratory nests.

Several of the samples of army ants from Panamá included large numbers of *Ereynetes* sp., but each of the two samples which contained over 100 specimens of this mite also included large amounts of dirt. Berlese funnel extractions of soil and leaf litter samples from refuse deposits and other areas near army ant colonies indicate that Ereynetidae are present in these areas but not in large numbers. It is unlikely that the small amount of dirt included with the ants could account for the presence of over 100 mites. Some of the mites were also found with ants aspirated from emigration columns. These also may have been picked up from the dirt, but this seems less probable than that they were on the workers. Therefore, it is concluded that Ereynetidae are found on the army ants, that they ride on the ants in the emigration columns, and have some unknown association with these and other species of ants.

Acaridae

No adult Acaridae were found in sufficient numbers in any of the samples of army ants to warrant their consideration as myrmecophiles.

However, some peculiar deutonymphs or hypopi were repeatedly found, and these are referred to here as a new genus A including four species. Nine additional species of acarid hypopi were found with the ants, but these are less likely to be myrmecophiles. The most outstanding characteristics of genus A are: the gnathosoma is more than twice as long as wide; the dorsal surface of the gnathosoma bears an elongate process with two long plumose setae; an anterior dorsal plate completely covers the gnathosoma; the anterior dorsal plate is one half to one third the length of the posterior dorsal plate, and both dorsal plates bear long plumose setae; legs III and IV are close to the posterior margin of the mite; and the venter is bent near the base of coxae III so that the area between legs III and the posterior margin is tilted dorsally. The shape suggests that this genus of hypopi may ride on a specific part of the ants; however, none was seen on an ant.

Acarid hypopus A-1 was found frequently with *E. burchelli* from Panamá (ratio of 346:503,620 or 1:1,456) and from British Guiana (ratio of 10:6,602 or 1:660). Only three specimens were found with other hosts: one with *E. hamatum* and two with *L. praedator*. One might assume that these hypopial mites would cling to any ant which is found on the forest floor. The fact that species A-1 shows a distinctly higher incidence with *E. burchelli* suggests that either these mites are selective or more probably they are restricted to a habitat where *burchelli* is more common.

Acarid hypopus sp. A-2 was not as restricted in its hosts. The following numbers of specimens were taken with these hosts: 9 (*E. hamatum*), 7 (*dulcius*), 42 (*vagans*), 4 (*L. praedator*), 1 (*Neiv. pilosus*) and 2 (*Neiv. gibbatus*). The incidence of mites with this distribution of hosts shows no clear pattern, although the absence of species A-2 with *burchelli* and the relatively high numbers with *dulcius* and *vagans* are significant. Species A-2 was found with four colonies of *vagans*, but only a single mite was taken with three of these. Species A-3 and A-4 are each represented only by a single specimen; the former with *L. praedator*, the latter with *Neiv. legionis*. Additional collections will probably show that this genus is associated with the army ants in some way and that additional species are found with other hosts.

Anoetidae

Like the family Acaridae, the Anoetidae are represented almost exclusively by deutonymphs or hypopi in the ant samples. At the present time there is less evidence that any of the Anoetidae are myrmecophilous than that for the acarids. However, two species were taken much more frequently than the remaining 15 species of anoetid hypopi. Species 8 was taken with samples from seven colonies of *burchelli foreli* from Barro Colorado Island and with one colony of *b. cupiens* from British Guiana. One of these samples was from a refuse deposit, and the remaining samples were all taken from bivouacs. Anoetid hypopus species 11 was found with seven hosts but only was common with *vagans*. Of the total of 54 specimens, 29 were found with five colonies of *vagans*. These host records suggest that the mites have some association with the army ants.

Hypochthoniidae

I am not aware of any reports of Oribatei having been found with ants. However, at least one species of Hypochthoniidae (det. T. A. Woolley) was found in fair numbers with *Noma. esenbecki*, and other species were found less frequently with other hosts.

Summary and Conclusions for Acarina

More than 8,000 mites which appear to have some association with the Ecitonini were found in this survey. Most of these are myrmecophilous in the sense that they are parasitic or phoretic on the ants, or are carried by the ants. The Acarina have been largely neglected in past studies of myrmecophiles, even though they are much more abundant in numbers of individuals than the myrmecophilous insects. The number of species of mites approximately equals the number of species of myrmecophilous insects found in the colonies studied. Although many species of both mites and insects were rare in the colonies of army ants, some of the species of mites are much more abundant than any of the myrmecophilous insects. The ratio of all mites to myrmecophilous insects was greater than 100:1 in some samples. The ratio of mites to ants for the entire survey is about 1:100, but in some samples it was as high as 1:4. Because most of the insects were collected individually, the ratio of the number of ants per myrmecophilous insect for the entire survey would not be comparable.)

Although other groups of ants have not been extensively sampled, the degree of host specificity within the Ecitonini suggests that most of these mites are restricted to the Neotropical army ants. The degree of host specificity is clearly highly variable with some species probably completely restricted to a single host. Presumably these could not survive with other hosts, or there is no method by which they could be transferred from one host to another. Other species, though they may be found with several hosts, usually show a "preference" or a higher incidence with one host than another.

Among the mites found with more than one colony, fifteen species were found with a single host. These species are macrochelids spp. 2, 3 and 7; neoparasitid sp. A-3; *Laelaspis* spp. 1 and 7; *Planodiscus* spp. A-2 and A-6; circocyllibanid spp. B-1 and B-2; *Coxequesoma* sp. 1, coxequesomid sp. A-1; *Perperipes ornithocephala*, *Perperipes* sp. 1; and Anoetid sp. 8. The Macrochelidae is the only family in the above list which includes no species found with two or more hosts. The above species of mites which seemed limited to single hosts were found with *Eciton* spp., *L. praedator*, *L. coecus* and *Noma. esenbecki*, showing that there is no single unusual host with an associated group of mites restricted to it.

The mites found with two hosts show more interesting relationships. *Acinogaster marianae* and neoparasitid sp. A-1 were found with both *burchelli* and *hamatum*. This might be expected since these two ants have been considered closely related in both morphology and habits. However, *Myrmecodispus dorylinus* and *Planodiscus* sp. B-1 were found with both *burchelli* and *vagans*, *Circocylliba* sp. 2 was found with *burchelli* and *mexicanum*, and Parasitoidea A-1 was found with *burchelli* and *praedator*. The last host relationship may result from the similarity of raiding behavior of the hosts, but no similar interpretation can be given for the other pairs of hosts.

Neoparasitid sp. A-2, *Circocylliba* sp. 4, *Myrmecodispus* sp. 1 and *Parapygmephorus* (*Petalomium*) spp. 8 and 10 were each found with both *dulcius* and *vagans*. These two hosts are more closely related morphologically (and to some extent in habits) than any other two species of *Eciton* from Barro Colorado Island. In this connection, it should be mentioned that the two species of Macrochelidae which attach to the tarsi of the workers are found only with these two hosts. Other mites found only with two species of host are neoparasitid sp. A-4 found with *L. praedator* and *Noma. esenbecki*, and *Planodiscus* sp. B-5 found with *hamatum* and *vagans*. The former case agrees with several closely related myrmecophilous insects which are found with these two hosts, and thus, is further evidence of a possible relationship between *Nomamyrmex* and *Labidus*. There is no morphological or behavioral evidence for a close connection between *hamatum* and *vagans*.

Adequate samples are not yet available to show how the species of mites or ants may vary throughout their geographical ranges. In a few cases ants of the same species were examined from localities at least 1,000 miles apart. These include large samples of *hamatum* and *vagans* from México and Panamá, and *burchelli* from Panamá, Trinidad, British Guiana and Brasil. Borgmeier (1955) has placed specimens of these species from the above localities in separate subspecies in all cases except *hamatum*. He was unable to divide the latter species into subspecies, even though it has a geographical distribution comparable to that of the other species. In a few cases, identical species of mites were found from two or three of these widely separated areas. However, in more cases the mites from these localities were distinct. Thus, the mites show more geographic diversity than their hosts.

The species of Uropodina which are most highly modified from the supposedly primitive type closest to Uropodidae (*s. str.*) are the species which are most restricted as to their hosts and their positions on the ants. Many of these are among the rarest species, for example, *Circocylliba* sp. 4, circocyllibanids sp. C-1 and D-1, and the coxequesomids. No clear tendency in this respect is shown by the much more homogeneous family Planodiscidae.

In every case in which mites have been seen at least several times on the ants, there appears to be some preference for certain parts of the ants. This statement holds true for all the groups and is not dependent upon a large amount of morphological specialization adapting the mite for riding in the particular position. For example, macrochelids spp. 2 and 3 both attach to the apices of the tarsi of workers. Neither species shows any obvious adaptation of the gnathosoma differing from free-living Macrochelidae. One of these two species has enlarged hind legs, though both seem to have identical habits. Among the additional examples of phoretic or parasitic positions the following are some of the most interesting: *Planodiscus* spp. ride only on the under surfaces of tibiae on workers. *Circocylliba* sp. 4 rides only on the inner surfaces of the mandibles of major workers, and Neoparasitidae sp. A-1 attaches to the membrane next to the mandibles of the majors. The most generalized species of *Circocylliba*, species 1, which is found with the largest number of hosts, is found also in a greater variety of positions (several positions known for head, thorax and abdomen).

Regardless of the genus of host, it is clear that most of the mites are on the largest of the polymorphic workers. Thus, the number of available hosts in any one colony of army ants may be only a small fraction of the total ant population. If the mites are restricted to major workers, the number of available hosts in a colony of army ants may be less than one per cent of the colony. Even an individual worker ant can be considered to be a group of microhabitats for mites. By adaptation to a specific part of an ant, a species of mite would avoid some competition with other mites. Therefore, future work with these mites should pay more attention to the exact position of the mites and the number of available positions on single workers of various sizes. Thus, a mite like Planodiscus may have four potential phoretic positions on a worker, whereas Circocylliba may have only two. Although the mites are limited in where they can attach to the ants, it should be pointed out that far less than 100% of the available phoretic or parasitic positions were occupied by mites in the colonies studied in Panamá.

As shown above, no colony had an extremely high mite population. The incidence of all mites rarely was greater than 1:10 ants and usually was closer to 1:100. For an individual species of mite the ratio is usually closer to 1:1,000 ants. Even with such a low incidence a single colony could have about 1,000 individuals of that species of mite . Such a low incidence might have some debilitating effect on a colony but presumably would not have a serious effect on the ant population. No species of mite was ever seen to be attacked by an ant, and perhaps the populations of mites within the colonies are limited primarily by the nomadic habits of the ants. Mites remaining at bivouac sites after the ants have departed and mites which drop off the ants must have difficulty getting to other colonies.

Over 80 new species of mites were found in this survey, and many belong to new genera. The large number of species, the diversity of these species, and especially the presence of species more highly specialized morphologically than the mites known from nondoryline ants, all suggest that each genus of Ecitonini may have a greater number of myrmecophilous mites than most nondoryline genera of ants. A similar relationship seems to hold for the numbers of myrmecophilous insects. Comparative examinations of samples of other ants from Panamá were not extensive enough to shed much light on this hypothesis. Moreover, since ants primarily from one locality and about 12 out of 140 species of Ecitonini have been sampled, one can predict that only a small fraction of the mite fauna existing with these ants has been found. Because both the Neotropical and the African doryline colonies have many species of myrmecophilous insects living with them, one would expect that in view of the mite fauna outlined here from the Neotropical species, the African species must have a similarly vast number of undescribed myrmecophilous Acarina.

Diplopoda

Before this study, two species of millipeds, *Yucodesmus dampfi* Chamberlin and *Calymmodesmus sodalis* Schubart, had been described from specimens found in columns of *Labidus praedator* (F. Smith). Five additional species and one more genus of Stylodesmidae were found on Barro Colorado Island with *L. praedator sedulus* Menozzi and *Nomamyrmex esenbecki crassicornis* (F. Smith). Two other species of *Calymmodesmus* were taken with *L. praedator s. str.* by Schneirla in México. The genera *Yucodesmus* and *Calymmodesmus* include several species which were found in caves and presumably are not associated with ants. I wish to acknowledge the help of Mr. H. F. Loomis who has identified and described these species (Loomis, 1959).

It is noteworthy that up to the present time no myrmecophilous millipeds have been found with any genus of army ants other than *Nomamyrmex* and *Labidus*. These two genera of army ants have been considered closely related by Borgmeier (1955) and earlier authors, and many myrmecophilous genera are found with both hosts. All known specimens of these millipeds were found with two colonies of *Nomamyrmex* and seven colonies of *Labidus*. Because I have watched over five times as many colonies and emigration columns of *Eciton* spp. on Barro Colorado Island, I believe it is safe to state that millipeds are not found with *Eciton s. str.* in Panamá. Millipeds are probably not found with *Neivamyrmex*, but emigration columns of this genus have been observed infrequently. None of the three genera of myrmecophilous millipeds found with Ecitonini has been found with any other tribe of ants.

The myrmecophilous millipeds belong to: *Calymmodesmus* Carl, *Yucodesmus* Chamberlin and *Rettenmeyeria* Loomis. *Yucodesmus* may be a synonym of *Calymmodesmus* as has been suggested by Loomis (1959: 2), but it is considered at least a subgenus by Causey (1960: 276). On the basis of the limited observations which have been made by Dampf (in Chamberlin, 1947: 101-102), Nevermann (in Schubart, 1953: 437-438) and myself, it appears that all three genera and all the species have similar behavior. Since my most extensive notes concern *Calymmodesmus*, this genus will be discussed first; and the subsequent genera will be compared with it. In my field work the species of millipeds were not distinguished, but later identifications showed that all the observations given below were made on at least three species.

Calymmodesmus Carl

Seven species of *Calymmodesmus* have been found with Ecitonini. Although all of these millipeds apparently live within the nests or at the periphery of bivouacs of the army ants, it is doubtful that they *must* live within the colonies. Most specimens lived for at least two months in laboratory nests or dishes without army ants. No other myrmecophiles taken in Panamá could be kept so successfully in the laboratory. Like other millipeds, these species appear to be scavengers on organic material and probably do not eat refuse from the booty of the army ants except for fluids or minute particles mixed with soil. By living in the ant colonies they may be protected from predators or parasites. There is no indication that the ants feed on the millipeds or on any secretion from them. However, workers often carry the millipeds during emigrations of the colony. Because the millipeds run or are carried in the emigrations and their hosts range from México to Argentina, one would predict a comparable distribution for the millipeds. Although species of *Calymmodesmus* were neither attracted to nor ate fecal material or booty refuse of

Nomamyrmex, these diplopods may help keep the nests of the ants clean. Since the army ant colonies periodically remain in one place for a statary phase of about three weeks, and possibly much longer in the case of the two host genera, scavengers which continuously ingest the dirt around the bivouac could be important for preventing the development of mold or fungi detrimental to the army ants. In the laboratory, Calymmodesmus readily ate dirt whether or not it was from near army ants, and presumably they extracted food from this dirt since they lived about three months. Millipeds kept with only moist paper, cotton, and fecal material of their host died in about one week. In dishes in the laboratory none of the millipeds was attracted to booty of the army ants, the ants themselves, Limulodidae, or Staphylinidae (Vatesus rettenmeyeri Seevers, V. schneirlai Seevers, or Ecitochlamys sp.). None of these insects was seen to lick the millipeds, but Calymmodesmus cleaned its own ventral surface, lateral lamellae, and legs. When moist filter paper, cotton and dirt were all in the same dish, the Calymmodesmus congregated on the dirt. From the above observations I would have predicted that Calymmodesmus would be most abundant at the beginning and ends of emigrations. Phoridae and some Staphylinidae which are more common around the periphery of bivouacs or in the refuse deposits are more common at the beginning and ends of emigrations. However, at my observation point, Calymmodesmus was much more abundant at the peak of the emigration when the queen and brood emigrated. The only detailed observations on an emigration of Nomamyrmex esenbecki were made on colony E-164 during 18 and 19 May 1956. This colony had a strong raid column which may have been an abortive emigration between 1:00 and 10:00 a.m. (18 May). During this period 27 millipeds were seen, but most of these were in the column when there was the maximum number of workers on it rather than while the number of workers running out from the bivouac was increasing. On the following evening the column shifted from a raid column to an emigration column between 7:15 and 8:45 p.m. During this 90-minute period only two millipeds were seen (at 8:12 p.m. and between 8:30 and 8:35 p.m.). The amount of ant traffic increased between 8:45 and 9:45 p.m., and four millipeds were seen during this hour. Between 9:45 and 10:45 p.m. the worker traffic was at its maximum, brood was carried, and the queen emigrated at 10:28 p.m. During this hour 170 millipeds were seen. During the following 45 minutes, although the ant traffic remained about the same, the number of millipeds decreased to 89. The following morning while the emigration column was becoming progressively thinner, the number of millipeds decreased. During somewhat less than half of the emigration of this colony, 299 millipeds were seen in the column. Over 90% of these were <u>Calymmodesmus</u> and less than five specimens were being carried by workers.

As can be seen in figures 27 and 28, <u>Calymmodesmus</u> and <u>Rettenmeyeria</u> have large lateral lamellae extending nearly horizontally and far beyond the ends of the legs. The arched dorsum of the body has a row of bumps (visible in figure 29) along each side of the body at the bases of the lateral carinae. The workers grasp the millipeds with their mandibles against the rows of bumps and carry them under their bodies in the same way that they carry their booty and brood. The ants were never seen to carry them by grasping the lateral lamellae or any other structures. About ten per cent of the millipeds were examined closely enough to determine that they were being carried with their anterior ends forward. This orientation may have resulted from the worker's picking them up while the millipeds were running in the emigration column. The worker ants ran faster and frequently passed the millipeds. Sometimes an ant passing over a milliped picked it up. An increasing number of callow and older workers were carried toward the ends of emigrations, but there was no indication that the proportion of carried millipeds increased toward the end of an emigration. Calymmodesmus runs in the centers of emigration columns, not along the edges as do some myrmecophiles. As one of them runs along, the head and first two to four body segments are frequently lifted somewhat off the ground (see figure 27). This position may facilitate the milliped's being picked up by an ant. It is not known whether the workers pick them up in the bivouacs. However, in laboratory nests the ants repeatedly ran over the millipeds without picking one up. (No tests were made with circular columns of ants in the laboratory.) A higher proportion of the Calymmodesmus was carried in columns of Labidus than in columns of Nomamyrmex. One might expect that since the average size of workers of Nomamyrmex is larger than that of Labidus, the millipeds would be more easily and frequently carried by the larger species. The maximum percentage of Calymmodesmus seen carried in columns of L. praedator was about 15%.

Where there were no ants for 15 to 30 cm. along an esenbecki trail, I watched about ten Calymmodesmus follow without hesitation the chemical trail of the army ants for distances of over 50 cm. Although the millipeds meandered, apparently touching opposite sides of the chemical trail, they appeared to get off the trail completely on only a few occasions. When one specimen ran about five centimeters from the main trail but possibly along a branch trail, it immediately turned and resumed following the emigration route with no difficulty. Two millipeds were taken as they ran along a trail ten minutes or more after the last ant was seen to pass. This column probably was the end of an emigration, but it may have been a raid column. Presumably *Calymmodesmus* uses its antennae to detect the chemical trail, but no observations were made on individuals with amputated antennae. One of the characters added to the generic description by Loomis (1959: 1) is the presence of a dense ventrolateral pad of hairs at the distal ends of the fifth and sixth antennal segments. The pad on the fifth segment is about one fourth the length of the segment, that on the sixth is slightly smaller but occupies almost the entire length of the shorter segment. These pads consist of numerous short, blunt setae which are so closely spaced that their bases touch. Their shape and thin walls suggest that they are chemoreceptors. The seventh segment has a few similar setae on the outer ventral part. The eighth and most distal segment has four much larger cone-shaped setae at the tip; these may also be sensory setae.

Since the hosts usually emigrate on the surface of the ground only at night, millipeds would not have to change their usual activity patterns to adapt to myrmecophily. However, sometimes the emigrations continue into daylight without evident disturbance to the millipeds. On two occasions as late as 10:30 and 11:00 a.m., *Calymmodesmus* was seen running in bright sunlight for distances up to 20 meters.

All specimens of *Calymmodesmus* which we collected in Panamá were found between 18 May and 5 June 1956. Two additional specimens were taken by Mr. William Lundy on 21 October 1956 near the Madden Dam, Canal Zone. Since the emigrations of the hosts are found more frequently during the rainy season (May to December), one can predict that most records of *Calymmodesmus* will also be in that period. Presumably the millipeds are in the colonies throughout the year.

Records. No distinct characters are known for identifying the females of *Calymmodesmus*. A total of 115 females of *Calymmodesmus* was collected, and 75 of these could not be identified. One unidentified specimen was taken from a raid column, and 45 were found in emigrations of small parts of two colonies of *L. praedator*. The remaining 29 females were found in the raid and emigration column of colony E-164, *Nomamyrmex esenbecki crassicornis*. Additional details for localities and the number of specimens collected of the species below can be found with the original descriptions.

Calymmodesmus andinus Carl. This species was found in Colombia, but no association with ants is mentioned with the original description.

C. biensifer Loomis. One male and the posterior end of a second specimen were taken in Oaxaca, México, by T. C. Schneirla. Unfortunately, the name of the host (*E. burchelli*) for this milliped and for *C. mexicanus* was incorrect as published by Loomis (1959: 4-5) (based on information he received from me). Schneirla (*in lit.*) has corrected the host to *L. praedator*. Both species of millipeds were taken from the area of a bivouac containing pupal worker brood scattered in chambers about 25 cm. deep.

C. carli Attems. This species was described from Guayaquil, Ecuador, with no mention of a possible association with ants.

C. falcatus Loomis. Since only three males of *C. falcatus* were found, this species was the least common of the species of *Calymmodesmus* found with *Nomamyrmex esenbecki* (colony E-164).

C. formicatus Loomis. *C. formicatus*, the largest species of *Calymmodesmus*, was one of the most abundant in colony E-164 of *Noma. esenbecki*.

C. gracilis Loomis. *C. gracilis* and *rettenmeyeri* were both found with *Noma. esenbecki* and with several colonies of *L. praedator*. On the basis of this limited survey, it appears that these two millipeds are more abundant with *praedator*.

C. inquinatus Causey. *C. inquinatus* Causey (1960) was found in a Guatemalan cave with no indication that it was associated with ants.

C. mexicanus Loomis. This species was found with *L. praedator* in México, and all comments given above under *C. biensifer* apply also to *C. mexicanus*.

C. rettenmeyeri Loomis. This species was common with *L. praedator*, but ten specimens were also found with *Noma. esenbecki*.

C. sodalis Schubart. Nevermann collected *C. sodalis* as it was running in a column of *L. praedator* in Costa Rica. Apparently large numbers of millipeds were seen, but the type series consisted of only three specimens (Schubart, 1953).

Rettenmeyeria parvipes Loomis

The genus *Rettenmeyeria* includes a single species, *parvipes*, found with *Noma. esenbecki*. Millipeds were found with only two colonies (E-160 and E-164) of this host. All eight specimens taken with colony E-160 are *Rettenmeyeria*, whereas only three out of 79 specimens of millipeds taken with colony E-164 belong to this genus. *R. parvipes* ingests soil, runs in the center of the emigration columns and can folow the chemical trails of the ants when no ants are present. Like *Calymmodesmus* spp., *Rettenmeyeria* both ignored and was ignored by workers and myrmecophilous staphylinids from the host colony. *R. parvipes* lived for three months in the laboratory without any ants. Even after this milliped had been isolated from its host for a week, it did not seem to be attracted to detritus or dead workers from a laboratory nest of *esenbecki*.

Yucodesmus Chamberlin

Yucodesmus alienus, *isidricus*, *murustunicus* and *viabilis* were described by Chamberlin (1938) from specimens taken in Mexican caves and apparently not found with ants. *Y. dampfi* Chamberlin (1947) was found in Vera Cruz, México, in a column of *L. praedator*. The column was watched at about 8:00 a.m. when there was much booty in it, but the column could have been either a raid or an emigration column. Since Dampf collected 15 specimens during a half hour, this colony like those of Barro Colorado Island probably contained several hundred diplopods. The millipeds were in the center of the column and were running much more slowly than the workers (Dampf in Chamberlin, 1947: 101-102). Apparently none of the millipeds was seen being carried.

Cynedesmus trinus Loomis

In addition to the myrmecophilous species discussed above, two other species were associated with army ants on Barro Colorado Island. One male of *Cynedesmus trinus* Loomis (1959: 5-6) was aspirated along with workers from a raid column of *Eciton mexicanum panamense* Borgmeier. (It was not found with *Neivamyrmex* as stated by Loomis.) The workers were carrying a large amount of booty, and this milliped was most likely booty captured by the army ants. The milliped was being carried, but both a myrmecophilous milliped and one which is booty can be carried in the same manner. No other specimens were found in 27 raid and six emigration columns of *E. mexicanum* observed during this study. *C. trinus* has been reported from two localities where it was not associated with ants (Loomis, 1959: 5; 1961: 97). Cynedesmus includes four other species, one of which, formicola, was found "in the nest of ants" on Grand Canary Island (Cook, 1896: 267). These ants could not have been army ants since Ecitonini are not found on the Canary Islands. Perhaps this genus includes both myrmecophilous and nonmyrmecophilous species.

Prionodesmus fulgens Loomis

Two specimens only 4.0 mm. long were found among arthropods from refuse deposits of Eciton burchelli. It was first thought that these might be myrmecophiles, but no additional specimens were found in 115 samples of material from refuse deposits of army ants. Since 11 specimens were found by H. F. and E. M. Loomis in habitats other than refuse deposits (Loomis, 1959: 7), this species is presumably not associated with the army ants but was probably found by chance in a refuse deposit.

Thysanura

Whenever myrmecophilous and termitophilous Thysanura have been extensively collected, most species have been found with several species of hosts. This generalization is valid for the three species found with army ants on Barro Colorado Island. However, one of the three species appears to be found primarily with the genus *Eciton* *s*. *str*., and a second species appears to be found primarily with the closely related genera *Labidus* and *Nomamyrmex*. According to the classification by Remington (1954), these species are placed in the subfamily Atelurinae in the Nicoletiidae. All members of the family lack eyes and are either subterranean or live in colonies of ants or termites. The Atelurinae have caudal filaments usually less than one-half the body length and antennae usually less than two-thirds the body length (Remington, 1954: 284). These characters are probably adaptations for living in colonies of social insects. Observations by Pohl (1957), who reviews most of the literature on the behavior of myrmecophilous Thysanura, Janet (1896) and Escherich (1905) suggest that all myrmecophilous members of the order have similar habits. However, as far as I can determine there have been no published observations on the behavior of Thysanura found with Ecitonini. The following observations can serve as a basis for more detailed experimental work in the future.

I am indebted to Dr. P. Wygodzinsky for determining all the specimens of Thysanura collected during this study, for describing one new species, and for supplying several references.

Trichatelura manni (Caudell)

The most common species of Thysanura found within army ant colonies in Panamá and probably throughout all of the Neotropical region is *Trichatelura manni* (Caudell, 1925) (see figures 31 to 38). Previously this species had been reported from Bolivia with *Eciton vagans* (Olivier), from Brasil with *Eciton dulcius dulcius* Forel and *Labidus coecus* (Latreille), and from Costa Rica with *E. hamatum* (Fabricius) and *E. burchelli* (Westwood) (Wygodzinsky, 1943: 262; 1958: 119). The hosts in Panamá include all five common species of *Eciton s. str.* found there: *hamatum*, *burchelli foreli* Mayr, *vagans mutatum* Borgmeier, *dulcius crassinode* Borgmeier, and *mexicanum panamense* Borgmeier. Although *T. manni* was not abundant in any of the colonies studied in Panamá, several specimens were usually found in every emigration column of *Eciton* which was watched for an hour or more. A total of about 54 males, 53 females and 37 immature individuals was found with all hosts. (The totals for males and females include some individuals which probably were not sexually mature, and the immature total refers to specimens too young for their sex to be determined.) The host data indicate that *T. manni* is distributed approximately equally among the various species of *Eciton*. The army ant genera *Labidus*, *Nomamyrmex* and possibly *Neivamyrmex* have been sampled enough to conclude that this thysanuran is rare or absent with them.

Three specimens of *T. manni* were found in samples of workers from bivouacs, two were taken from raid columns, and all the remaining specimens were found in emigration columns. The dearth of specimens in samples of workers is attributed mainly to the workers' killing all Thysanura if they are placed together in a container while the ants are disturbed. *T. manni* was seen about ten times in the bivouacs of *hamatum* and *burchelli*. On these occasions individuals were running in the central mass of larvae. Presumably the thysanurans stay in this section where the ants are more quiet compared with areas of the bivouac where raiding workers are constantly running in and out. When one attempts to collect a few hundred or a few thousand workers and larvae from a bivouac, the extremely agile Thysanura can readily escape. *Trichatelura*, like most myrmecophilous insects, was found so rarely on diurnal raid columns that we ceased to watch these columns except for brief periods. The only *T.* manni found on a diurnal raid column was an immature specimen seen at 10:38 a.m. with *E. burchelli*. The thysanuran and more than 90% of the workers were running toward the bivouac at that time. It is not known whether the thysanuran had previously left the bivouac. A few *T. manni* were found on nocturnal raid columns of *E. burchelli* or *mexicanum*. Since *T. manni* moved away from light in the laboratory, I would expect that light may be important for keeping the Thysanura inside the bivouac during the day when *burchelli* does most raiding. However, at night the Thysanura may not be able to distinguish between raid and emigration columns if the traffic is primarily going away from the bivouac. Between 6:30 and 7:30 p.m. individuals of *T. manni* were seen along columns to spinning clusters about a meter from a bivouac, but promptly returned to the bivouac.

Most specimens of *manni* were seen running in the centers of emigration columns during the time of maximum ant traffic when brood was being carried (see figure 31). No specimen was ever seen near the end of an emigration. The workers were never seen to carry any species of Thysanura, and it is doubtful that the ants could carry such large, smooth, soft-bodied insects without injuring them. *T. manni* was occasionally seen riding on the workers themselves but more frequently rode on large larvae or booty being carried by the ants. The adult thysanurans appeared to be too large to ride on the running workers without being knocked off. A smaller individual usually clung to both the ant's gaster and the object carried by the ant. One emigration of *E. vagans* included numerous alate males, but only one out of about six *manni* was seen riding on a male.

Several times *T. manni* was seen running in emigration columns in the opposite direction from the majority of ants. Each thysanuran held its anterior end higher than it did when moving with the emigrating ants and appeared to be attempting to catch onto one of the running ants or onto larvae being carried. For more than ten minutes one thysanuran persisted in this behavior while constantly being kicked over on its back and pushed along by the workers. Several times it was turned around by the ants and started to run toward the new bivouac, but each time the thysanuran again reversed itself. It progressed about 60 cm. toward the old bivouac in ten minutes, and the subsequent fate of this individual is unknown. Some Limulodidae showed similar behavior in emigration columns.

Thysanura were not kept alive in the laboratory for more than 11 days; and if they were kept with less than 100 ants in small dishes, they died more quickly. Consequently, there is no direct data on the length of the instars or life cycle of *Trichatelura*. Specimens were taken throughout the entire period of field work from February through August and showed no clear seasonal fluctuation. However, even though a few immature specimens were taken at the end of the nomadic phase, most of them were taken on the first nomadic day. Since the smallest individuals were also found on the first nomadic day, these data suggest that *T. manni* lays eggs during the statary period and may have a reproductive cycle synchronized with that of the host.

Specimens of *Trichatelura manni* drank water from paper or cotton and fed on fluids oozing from the booty of the army ants. They were never seen to puncture any of the soft larvae or pupae of the army ants or their booty. The thysanurans also appeared to feed on surface secretions or particles scraped off larval army ants, adults and booty (see figure 38). The thysanurans often appeared to be cleaning the bodies of the workers in the same manner as *manni* cleans its own legs. Most frequently *manni* cleaned the legs of the workers, presumably because it could most easily reach these parts of the ants from the floor of a laboratory nest. After spending 30 seconds to about a minute rapidly strigilating (in the sense of Wheeler, 1910: 393) over the surfaces of a leg, *manni* sometimes continued up on the body of the ant. At times a worker stood quietly, as in figures 35 and 36, and allowed the thysanuran to climb all over her and clean the dorsal and lateral surfaces of her body. The thysanurans cleaned the scape but were not seen to clean the area around the mouthparts of the workers or any of the ventral surfaces of the body. Unlike some histerids, *T. manni* did not appear to be particularly attracted to the shiny heads of the major workers of *E. hamatum*. When several *T. manni* were placed in a small laboratory nest with a queen and ten to 100 workers of either *E. burchelli* or *hamatum*, the thysanuran showed no more attraction toward the queen than toward the workers. However, when similar observations were made with two queens of *vagans* and one of *dulcius crassinode*, the Thysanura were much more frequently found riding on the queens than on the workers and cleaned both legs and dorsal surfaces of the queens. Two or three out of four Thysanura were usually on these queens while three histerids, Latronister rugosus Reichensperger, and seven staphylinids, Vatesus panamensis (Mann), seemed to ignore the queens. The workers were also attracted to the queens and licked them, but none of the workers attacked any of the Trichatelura on these queens. The four T. manni kept with workers, booty and the queen of E. vagans from colony E-180 died within 48 hours, but no injuries made by the workers could be found on the thysanurans.

All the Thysanura are extremely agile and fast moving. T. manni can run faster than the workers of Eciton; when a worker darted toward it, an individual of manni could easily circle away. The thysanurans seldom ran in a straight line except in emigration columns, and they most frequently ran in a zig-zag manner, turning in tight circles when touched by an ant. T. manni readily turns in a circle with a diameter of one to two times its length. When a specimen of manni was cleaning the legs of a worker and the ant ran off, the thysanuran often pursued her. If a worker placed a leg on top of the abdomen of manni, a quick flip of the abdomen would usually dislodge it (see figure 32).

The workers sometimes attacked and killed the Thysanura in laboratory nests but at other times ignored them. The Thysanura escaped with no visible injury at least nine out of ten times when a worker appeared to bite them. Moreover, the workers often did not attack Thysanura which were dying and unable to walk or which were struggling to right themselves after being kicked on their backs by the ants. A specimen of manni taken with E. dulcius and kept in a laboratory nest with that host for eight days was then transferred to a laboratory nest of vagans.

The thysanuran immediately ran among the workers and cleaned their legs without being attacked by the _vagans_.

All Thysanura seemed constantly alert and moved frequently unless they had hiding places where the ants could not readily touch them. In some laboratory nests it is possible that _Trichatelura_ became exhausted from constant running. The most frequent resting place for _T. manni_ in laboratory dishes without hiding places was under a standing worker. Army ants commonly stood in one place for at least 30 minutes, and a thysanuran standing between the legs of the ant was protected from being stepped on by other workers. While resting under a worker, _T. manni_ faced in any direction.

It was surprising to find that _T. manni_ runs on the tips of its tarsi (see figures 33, 34 and 37). The body is held far from the surface, and the abdominal styli are held vertically as in figure 34. The long antennae and maxillary palpi are constantly extended in front of the head. Since the palpi are so large and are held near the ground, they rather than the antennae may be used to determine the location of chemical trails of the army ants. _T. manni_ was never seen on columns where the traffic was weak enough to compel the thysanuran to follow the chemical trails. In most cases the Thysanura could have tactually followed the ants themselves. However, when attempting to aspirate the thysanurans from columns, I sometimes missed a specimen and disturbed the column. At these times, _T. manni_ often hid under leaves for at least a few seconds and then followed the trail whether or not ants were on it.

Trichatelura borgmeieri Silvestri

The only other species in the genus *Trichatelura* is *borgmeieri* Silvestri (1932: 133-138) described from specimens taken with *Nomamyrmex esenbecki* (Westwood), *Noma. hartigi* (Westwood), and *Labidus praedator* (F. Smith) in Brasil. It has also been taken with *E. dulcius dulcius* Forel, *Neivamyrmex diana* (Forel) and *Neiv. minensis* (Borgmeier) (Wygodzinsky, 1943: 262). *T. borgmeieri* was usually numerous in the colonies of these ants (Silvestri, 1932).

Six males and six females of *T. borgmeieri* were found in an emigration column of *Nomamyrmex esenbecki crassicornis* (F. Smith) (colony E-164). All of these specimens were running in the column. Ten additional specimens were seen in the column but not taken. Because no specimens of *borgmeieri* were taken with *Labidus praedator* on Barro Colorado Island, it must be rare or absent there with *praedator*.

Grassiella rettenmeyeri Wygodzinsky

Grassiella includes at least 12 species which have been found either associated with ants and termites or apparently free-living in soil. The most recent revision includes seven Neotropical species in addition to the description of *rettenmeyeri* Wygodzinsky (1958) (see figure 30). A total of ten specimens of this species were found on Barro Colorado Island with *Nomamyrmex esenbecki*, *Eciton burchelli*, *E. vagans*, *E. dulcius crassinode*, *E. mexicanum* Roger and *Neivamyrmex gibbatus* Borgmeier. In addition, three specimens were found in leaf litter on the forest floor or running on the ground. The latter records and the wide range of hosts are typical for species which are not closely associated with ants.

Furthermore, *Grassiella* shows no morphological adaptations for myrmecophily except possibly the limuloid form which is similar to that of many free-living Thysanura (Wygodzinsky, 1958: 99). It is amazing that such a soft-bodied, fragile insect can live within the colonies of army ants. All specimens which were taken died a few hours after they were collected whether or not they were kept with ants. All specimens were taken with an aspirator, and at least half of them appeared to be stunned or permanently injured when captured. *G. rettenmeyeri* was found both during the day and night. The single specimen found with *burchelli* was running in the area of anastomosing columns just behind the advancing swarm front at about 11:45 a.m. The thysanuran may have just joined the column as the swarm front was advancing across the forest floor.

Two additional specimens of *Grassiella* sp. were taken with *L. praedator*, including one found by Schneirla in México. These could not be identified but may belong to *G. rettenmeyeri*. No previous records of *Grassiella* being found with *Labidus* are known to me.

Collembola

Over 300 specimens of myrmecophilous Collembola were found in samples of army ants taken on Barro Colorado Island. These are the first Collembola reported from Dorylinae. Beebe (1919: 464) reported seeing springtails within a bivouac of *Eciton ?burchelli* in British Guiana, but I could find no records of any specimens being collected or described. The myrmecophilous species found in Panamá belong to the Entomobryidae, subfamilies Cyphoderinae and Paronellinae. Many myrmecophilous and termitophilous species found throughout the world are Cyphoderinae. All the species from Panamá are new and not yet described. I am indebted to Dr. F. Bonet who has determined approximately half of the specimens and indicated which species he thinks are myrmecophiles based on their morphology and systematic position.

Work with myrmecophilous Collembola is made difficult since numerous nonmyrmecophilous species are invariably collected with ants. To minimize this problem, samples from a single bivouac or column were frequently kept in separate vials according to the amount of soil or debris included with the ants. Large numbers of springtails found in samples of ants containing little or no extraneous debris were considered myrmecophilous.

Tentative conclusions indicate that the most common springtail found with the Ecitonini is a new species of *Cyphoda*. This genus was previously known only from Africa. In addition, two species of *Cyphoderus* and one species of *Paronella* were found near army ants. *Cyphoda* was found with the following hosts: *Eciton hamatum* (Fabricius), *E. burchelli* (Westwood), *E. vagans* (Olivier), *Labidus praedator* (F. Smith), *L. coecus*

(Latreille) and Nomamyrmex esenbecki (Westwood). The maximum incidence of this species was in a sample of workers and male larvae taken from an emigration column of E. hamatum. About 50 Collembola were found with 120 workers and 68 male larvae. It is thought that the springtails may have been restricted to the larvae since a sample of 67 major workers placed directly into alcohol in the field contained no Collembola. Because other small myrmecophilous insects are more likely to ride on the majors than on smaller workers, the opposite size relationship would not be expected with Collembola. On an emigration column of Nomamyrmex esenbecki, the Collembola were actually seen riding on more than ten large workers. (No true major workers or soldiers of Noma. esenbecki can be distinguished.) The specimens seen were on the alinotum and on the posterior dorsal surface of the head. Probably the springtails rode in other positions where they could not be seen. This colony of esenbecki had large numbers of springtails in it while it had a brood of worker-producing larvae. Although hundreds of springtails must have ridden on workers or larvae, many others ran along the emigration trail. These Collembola ran in a zig-zag manner frequently going outside the margins of the emigration column.

In laboratory nests Collembola were occasionally seen running around among eggs and larvae. Probably they were feeding on substances on the surfaces of the larvae. It is clear from observations on about 150 colonies of army ants in Panamá that the population of Collembola in army ant colonies varies greatly. The incidence of Collembola in some colonies is less than one per 5,000 larvae, whereas in others it was about one per one or two larvae. It is doubtful whether the army ants are able to kill such small active insects. Desiccation and lack of food during the beginning of the statary period and predation by other myrmecophiles may control the population of Collembola in army ant colonies. Delamare-Deboutteville (1947: 456-457; 1948: 305-306) concluded that no Collembola are found with the African doryline ants (Anomma) because the nests of these ants were not permanent and did not have a suitable environment. The large numbers of Collembola found in colonies of Ecitoni in Panamá indicate that migratory habits are not necessarily prohibitive. Low humidity and perhaps high temperatures are probably the main limiting factors excluding springtails from the colonies of Anomma. It is of further interest that the order Collembola is the only major group of myrmecophilous insects found with Neotropical dorylines and not with African dorylines.

Hemiptera: Enicocephalidae

No species of Hemiptera has been reported to be a myrmecophile with colonies of Neotropical army ants. However, one species of Enicocephalidae taken near Lawrence, Kansas, may be associated with these ants. This species of *Systelloderes* (determined by R. L. Usinger) was found in a laboratory nest containing considerable dirt and about 10,000 workers of *Neivamyrmex* *nigrescens* (Cresson). The bug was aspirated as it was running along one of the ant trails in the laboratory nest, but no ants were on the trail at the time. It is the same color as the *nigrescens* which increases the probability that it may be a myrmecophile. The bug was not killed during the three days that it was in the nest perhaps mainly because there was a large amount of dirt in which it could hide.

Diptera: Phoridae

About 100 species of Phoridae have been reported to be associated with army ants, and most of these have been found within bivouacs or columns. No other Diptera are common myrmecophiles with Ecitonini. Some of the phorids are assumed to be parasitic on the army ants since the females have sclerotized ovipositors probably used for inserting eggs into the adult or larval ants. However, most of the myrmecophilous phorids have more membranous ovipositors and are probably scavengers in the booty refuse from the colonies (Borgmeier, 1928: 159). Almost all the phorids commonly found with army ants are females with vestigial wings, whereas the males, which can fly, are seldom seen. Unlike most of the myrmecophilous Staphylinidae and Histeridae, a large number of the phorids run in the refuse columns and along the edges of the bivouacs. Over 2,400 specimens belonging to about 34 species from Barro Colorado Island and two from Kansas were taken in association with Ecitonini. I wish to thank Father T. Borgmeier for determining these specimens and describing the new species. About 23 species are considered myrmecophilous since they were found in samples of workers from bivouacs or were running in the ant columns. Eight of these species were also taken in refuse deposits. No phorid was ever seen riding on an army ant or anything carried by the ants, and no phorid was seen carried by a worker. In the columns the phorids ran in the quick darting zig-zag manner typical of even the nonmyrmecophilous Phoridae. They avoided the center of the columns and often ran one to two centimeters from it but darted into the column periodically. Many times they ran directly away from the column (as in figure 14), but after a few centimeters they doubled back to it. The few times that observations were made on phorids in laboratory nests the flies ran around almost constantly. They did not appear to be attracted to the workers, brood or booty and avoided contact with all live insects.

The phorids were the most abundant family of myrmecophiles seen along raid columns, both day and night. Around bivouacs and refuse deposits of *E. hamatum* and *burchelli* the Phoridae were present throughout the day but became more numerous in the early evening. At that time many phorids left the bivouac and ran out along raid columns if an emigration had not yet begun. The number of phorids running out from the bivouac along raid columns decreased as the phorids joined the emigration column. The fewest phorids were seen in the middle of an emigration. Probably the decrease in the middle was not as pronounced as it appeared since these tiny flies are among the most difficult myrmecophiles to see in a crowded column. At the ends of some raid and emigration columns the number of phorids seen was astonishing. Following a swarm raid of *Labidus praedator*, 520 specimens of *Ecituncula* (*Labiduncula*) *halterata* Borgmeier were taken from three raid columns. Most of these phorids were running along the trails after all the ants had disappeared into holes in the ground. Over 2,000 phorids must have run along the three short raid trails during the ten minutes (11:57 a.m. to 12:07 p.m.) that I watched them. It is estimated that more than 5,000 Phoridae, almost all belonging to one species, accompanied the entire raid. Although this may be an atypical example, it was not unique since numerous phorids were seen in columns at the ends of other raids of *praedator*. It is not known whether these flies came from the bivouac or whether some had been in the litter on the forest floor and joined the columns during the raid.

At the end of emigration columns of *Eciton hamatum*, *E. vagans*, *E. dulcius*, *Nomamyrmex esenbecki* and *Neivamyrmex opacithorax*, we have also seen increased numbers of phorids. The most spectacular example was at the end of an emigration of *E. vagans* when there were as many as 100 phorids per meter of trail between 10:15 and 10:30 p.m. The last scattered workers passed the same point along the trail between 10:15 and 10:20 p.m. In this 15-minute period 494 Phoridae were taken belonging to the following species: *Ecitophora collegiana* Borgmeier (8♀), *Ecitophora varians* Borgm. (371♀), and *Thalloptera schwarzmaieri* Borgm. (115♀). An increase in the number of phorids at the end of an emigration was also observed at the end of two emigrations of *Neiv. opacithorax* in Kansas. However, large numbers of phorids were never observed with *Neiv. opacithorax* or *Neiv. nigrescens*. One emigration of *opacithorax* (colony E-263) was watched from 10:25 p.m. to 1:30 a.m. including about 35 minutes after the last ants had passed the observation point. During the period of about two and one-half hours up to 1:00 a.m. while the ants were still emigrating only two phorids were seen (at 11:18 p.m. and 12:31 a.m.). However, from 1:00 to 1:30 a.m. after all the ants had passed, four phorids were seen. The species were *Xanionotum smithii* Brues and *Acontistoptera melanderi* Brues.

At 4:00 p.m. after a cluster of *Neiv. opacithorax* left an area under a rock, four phorids, 33 staphylinids and only five ants remained. About two hours earlier over 1,000 workers had been seen under this rock. In a similar manner phorids and other myrmecophiles were found at bivouac sites of Panamanian species of *Eciton*. Few myrmecophilous insects could be found at any of these bivouac sites five to 20 hours after the last ants had left.

On one occasion when a raid column disappeared under some leaves, the bivouac location for a colony of *E. vagans* in Panamá was found by finding phorids hovering over several leaves. Some of the phorids landed; and when the leaves were removed, phorids and ants were found going in and out a hole in the ground. These phorids probably flew to this area, but some may have come from the bivouac. When it became dark about 6:45 p.m., the phorid activity stopped. At this hole two female and 15 male *Ecitophora bruchi* Schmitz were taken; this was one of the few occasions when male phorids were found in Panamá. In Kansas a specimen of *Megaselia* sp. was taken after it had landed on the ground and was running toward a hole being used by a column of *Neiv. opacithorax*. This genus has not been considered to be associated with army ants but appears to be attracted by them.

A few larvae and pupae of Phoridae were found in the refuse deposits around bivouacs, but no species was reared. Bruch (1923: 195) reported that phorid larvae [one species?] ate staphylinid and histerid larvae in refuse deposits.

A detailed list of host records will be postponed until Borgmeier finishes revisions of the myrmecophilous Phoridae. Several tentative conclusions can be made regarding the hosts: (1) the same two species of phorids are found both with *Neiv. opacithorax* and *Neiv. nigrescens* in Kansas and Texas; (2) one species is found with the five common species of *Eciton s. str.* but with no other host; (3) one species is not found with *E. burchelli* but is found with the four other common species of *Eciton*; (4) several species are restricted to a single host; and (5) *Neivamyrmex* spp. appear to have fewer phorids than *Eciton*, *Labidus* or *Nomamyrmex*.

Coleoptera

The order Coleoptera, in both numbers of species and numbers of specimens, is the most important order of myrmecophilous insects found with army ants. The families found, in order of decreasing abundance, are: Limulodidae, Staphylinidae, Histeridae and Pselaphidae. These families include the main groups of myrmecophilous Coleoptera. The most important group of myrmecophilous beetles which appears to be absent from the Neotropical army ants is the Clavigerinae (Pselaphidae). This subfamily is present but not abundant with the African dorylines.

Limulodidae

The family Limulodidae was proposed by Seevers and Dybas (1943) for some of the beetles formerly included in the Ptiliidae and in the staphylinid subfamily Cephaloplectinae. Although some of the hosts are unknown, the 27 species included in the family are considered to be obligate myrmecophiles, most of which live with army ants (Ecitonini and Cheliomyrmicini). All species are found in the Western Hemisphere except for the genus Rodwayia which includes six Australian species, none of which is known from doryline ants.

The species of Limulodidae range from about one to four millimeters in length, and their small size undoubtedly accounts for their scarcity in past collections of myrmecophilous insects. All limulodids are similar in appearance and when alive could be separated only by differences in size and occasionally by color (see figures 39 to 42). The type series of all species of Limulodidae together with the subsequent records published by Seevers and Dybas (1943) total about 300 specimens.

During this survey approximately 1,000 specimens were taken in Panamá, and about 100 more were found in samples of ants collected in various localities by T. C. Schneirla and N. A. Weber. These collections indicate that the majority of beetles found within colonies belong to the family Limulodidae. The family Phoridae is the only group of myrmecophilous insects exceeding the Limulodidae in number of individuals. However, in number of species the Limulodidae may be exceeded by the Staphylinidae, Histeridae and Phoridae.

The limulodids are so small that they are extremely difficult to determine. Specimens mounted on microscope slides are essential, but for such mounts these beetles are so large that dissections are necessary. Primarily because of these difficulties, all determinations are incomplete at the present time. I wish to thank Mr. Henry S. Dybas who is studying this material and has provided the tentative determinations used below. He has separated all specimens belonging to the genus *Cephaloplectus*, and these are currently being studied by Father T. Borgmeier. Since most observations were made on the behavior of *Cephaloplectus* in Panamá, this genus will be discussed first. Field numbers in parentheses will be cited to make it possible to connect observations with individual beetles or species.

Cephaloplectus spp.: Numerous specimens were taken with *Eciton burchelli*, *vagans*, *dulcius*, *mexicanum*, *Nomamyrmex esenbecki* and *Labidus praedator* on Barro Colorado Island. In addition, specimens were found with samples of *burchelli* taken in México, Trinidad and British Guiana by Schneirla or Weber. The most surprising conclusion from these host records is that *Cephaloplectus* is not found with *Eciton hamatum*. Nevertheless, *Cephaloplectus* was common with *burchelli*, the species of army ant considered most closely related to *hamatum*. Although no specimens of *Cephaloplectus* were found with *Labidus coecus* in Panamá, this host was not studied extensively. *C. trilobitoides* Mann is known from that host in Guatemala (Seevers and Dybas, 1943: 583). The apparent restriction of *Cephaloplectus* to species of *Eciton*, *Labidus* and *Nomamyrmex* is somewhat doubtful because *C. argentinus* Bruch was described from specimens found with "*Neivamyrmex hetschkoi* (Mayr)." The host probably was *Neiv. raptans* according to the interpretation by Borgmeier (1955: 475-476). The host and small size of *C. argentinus* suggest that it does not belong in the genus, and the original description is inadequate for determining the taxonomic position of this species.

Cephaloplectus sp. runs in the centers of emigration columns of *E. burchelli* but more frequently rides on booty, larvae or cocoons carried by the workers. Occasionally an individual was found riding on the workers themselves or on queens in laboratory nests or emigration columns. There was no indication that *Cephaloplectus* or any of the smaller limulodids rode in a balanced or symmetrical position as was reported for *Paralimulodes* (Wilson, *et al.*, 1954: 160). No limulodid was ever seen being carried by a worker. The percentage of *Cephaloplectus* riding on the larvae appeared to increase as the larvae grew larger. In an emigration of burchelli (colony E-136) on 30 March 1956 more than 90% of the limulodids (1589) rode on the larvae. (The first statary day following this emigration was 3 April.) *Cephaloplectus* usually emigrated during the period when the brood was carried regardless of whether the limulodids rode on the brood. No *Cephaloplectus* was seen at the end of an emigration when the column of ants had thinned or disappeared. If the traffic along a column was disturbed by mass collecting, most riding limulodids dropped to the ground, hid under leaves or ran along the trail. When the column was not disturbed, and the beetles fell off, they almost invariably ran in the opposite direction to the emigrating workers (1689, 2195? with *burchelli*, 1847 with *mexicanum*). While running against the traffic, the limulodids lifted their anterior ends higher than when following the emigrating ants. They seldom ran move than a few centimeters without stopping and arching their bodies. Several times these limulodids (1689) were seen to catch onto passing workers and ride off toward the new bivouac. Sometimes these attempts were quite unsuccessful with the same beetle falling off and being kicked and pushed backward a few times before it disappeared. Even with repeated difficulty these limulodids managed to get on a worker within 30 seconds, and the longest series of unsuccessful attempts lasted slightly over two minutes.

No *Cephaloplectus* was seen in a raid column of *burchelli*, but three individuals were seen riding on larvae being carried out to a spinning cluster between 6:35 and 7:53 p.m. Although most *Cephaloplectus* spp. were seen riding in emigration columns of *burchelli*, large numbers were seen running in columns of other hosts. About 55 specimens (1657) were seen in a raid column of *E*. *mexicanum* (colony E-147) between 7:40 and 10:00 p.m. Not a single limulodid was seen riding on the workers or on any of the thousands of pieces of booty in this column. Four additional specimens (1219) were seen running in a raid of the same host species (colony E-113) between 8:20 and 9:00 p.m. No major workers and little booty were seen in the latter column. The only *Cephaloplectus* (1847) seen along an emigration column of *mexicanum* was also running.

More than 50 individuals of *Cephaloplectus* (1595) were seen running in an emigration of *E. dulcius crassinode* (colony E-137) which had a brood of eggs and young larvae along with a few cocoons containing worker pupae. No *Cephaloplectus* was riding on a cocoon, on brood, booty or workers except for two seen on major workers. However, seven more were riding on the queen in this emigration (see figure 40). Most of the limulodids were in the early part of the emigration before the queen was seen. The queen emigrated quite early before most of the brood was carried. In another emigration of *dulcius* (colony E-204), *Cephaloplectus* (2077?) was seen riding on larvae.

In an emigration of *Labidus praedator* (colony E-177) two individuals of *Cephaloplectus* (1881) were riding on heads of large workers, and two were running. In an emigration of *Nomamyrmex esenbecki* (colony E-164) most limulodids ran, but a few rode on booty or army ant larvae, and at least 18 rode on the queen (see figure 41 discussed more fully below).

The above data suggest several conclusions: (1) All species of *Cephaloplectus* both run and ride during emigrations. (2) If the brood is at least half grown, most *Cephaloplectus* will ride on the brood. (3) If booty is numerous and brood is young or absent, some of the limulodids will ride on the booty. (4) The species of *Cephaloplectus* found with *Nomamyrmex esenbecki*, *Eciton mexicanum* and *dulcius crassinode* may have a greater tendency to run rather than ride compared with the species found with *E. burchelli*. (5) Individuals which have been riding, but which lose their positions, run in the opposite direction to the emigration and attempt to ride again, whereas individuals which have been running continue to run toward the new bivouac.

In an emigration of Nomamyrmex esenbecki (colony E-164) at least 21 ~~18~~ Cephaloplectus sp. (1831) were riding on the queen in addition to one small worker on her gaster. The limulodids covered virtually her entire dorsal surface. Although 18 limulodids stayed on her, probably two or three fell off when the queen was picked out of the column with forceps. In a small laboratory nest the limulodids stayed on the queen almost constantly. When the nest was jarred, most or all of the limulodids would leave the queen, but climbed back on her after running around the nest for a few seconds.

These limulodids usually faced anteriorly on the queen with their abdomens most frequently turned somewhat toward one side (see figures 41 and 42). These positions on the alinotum and gaster are probably the ones where Cephaloplectus is least likely to fall off. Frequently a Cephaloplectus ran onto the head, antennae or legs of the queen but rode there only for brief periods. Workers made no attempt to bite or remove the limulodids from their queen. Apparently because the limulodids did not allow the workers to lick the queen, there were few workers around her as long as the limulodids were present. The queen showed no reaction toward the limulodids even when the beetles ran out on a flagellum. Cephaloplectus rarely rode on the fourth gaster segment, and none was seen on the fifth (last) segment unless there was no room anteriorly. If only one to four limulodids were placed with the queen, these invariably rode on her first, second or third gaster segments. Most of the time the limulodids rode quietly on the queen with their mouthparts not touching her. However, occasionally they would lick her, and the limulodids which ran to other parts of the queen often licked her briefly in several places.

Several individuals of *Cephaloplectus* sp. (1354, 1797) taken from emigrations of burchelli (colonies E-110 and E-148) spent many minutes cleaning the queens from their host colonies. Each limulodid shifted position almost constantly, never spending more than about one second at any one point. It ran back and forth repeatedly and often touched the first and second gaster segments, petiole and head with its mouthparts. This species also cleans the legs and antennae of workers using the rapid strigulating movements typical of all limulodids which have been observed (see Park, 1933 and Wilson, *et al*., 1954). One individual cleaned the mandibles of a worker and rested for about one minute with its head between the worker's mandibles. Probably it was feeding on fluids around the mouthparts of the worker. *Cephaloplectus* also rode on the pronotum and elytra of *Vatesus rettenmeyeri* Seevers and cleaned the dorsal surface of the staphylinid more extensively than that of any worker. The *Cephaloplectus* apparently irritated the *Vatesus* which shook violently until the limulodid fell off. *Cephaloplectus* (1814) also rode on the abdomen of *Ecitochlamys* sp. in a laboratory nest but was not seen to clean this staphylinid.

In bivouacs and laboratory nests where larvae or cocoons of the army ant were present, *Cephaloplectus* could be seen running around among the brood and going over it with its mouthparts. One might expect that the limulodids would find remains of booty plus possible secretions from the larvae or workers on the surfaces of the larvae. However, the limulodids also were seen licking the surfaces of the cocoons. The only time the latter observation was made was on a first nomadic day by which time the old cocoons may have acquired some edible material on their surfaces, or the limulodid may have been attracted by the callow adults inside the cocoons. *Cephaloplectus* (1597) was seen feeding once on pupae of *Polistes* (given to the ants for food in a laboratory nest). No limulodid was ever seen in a refuse deposit, and the Berlese samples from these deposits indicate that *Cephaloplectus* and other limulodids are rarely found there.

The workers always ignored a *Cephaloplectus* when it was cleaning or riding on their backs. However, several times workers attacked limulodids running in laboratory nests. The shape of these beetles must be some protection against attacks by the ants and is probably an important adaptation facilitating their riding on the workers or larvae. These small beetles can ride on the sides or upper surfaces of larvae without getting in the way of the ant's legs. When a *Cephaloplectus* fell or was kicked on its back, it was momentarily helpless; and the workers could bite the legs and edges of its body. The workers on one occasion readily amputated the legs of a *Cephaloplectus*, rolled the limulodid across the floor of the nest, and attempted to sting it.

Limulodes (*Carinolimulodes*) *philovagans* *Seevers* *and* *Dybas*: Most observations on the behavior of Limulodidae of other genera are similar to those above made on *Cephaloplectus* spp. *Limulodes* *philovagans* was the most abundant of the smaller species. It was found with *E*. *hamatum*, *vagans* and *dulcius* *crassinode*. Although this species is about half the size of the largest *Cephaloplectus*, the majority of specimens seen in emigration columns was running. In a first nomadic emigration of *E*. *hamatum* (colony E-121), 26 specimens were seen between 5:58 and 7:18 p.m. Most of the brood was carried between 7:00 and 9:00 p.m., and the last workers emigrated between 9:15 and 9:30 p.m. It is strange that such small myrmecophiles would run on an emigration when much bigger ones often ride. Limulodes philovagans (2271-X) was also found riding on alate males in an emigration of E. vagans (colony E-240). A specimen of L. philovagans was also seen running in an emigration of hamatum (1638, colony E-141) on about the fourth nomadic day. It emigrated after the workers had started to carry the larvae. Two specimens were seen running in raid columns of hamatum (1157, colony E-105) between 6:59 and 8:34 p.m., and another specimen was found running in a raid column of dulcius crassinode (2010, E-194) between 5:20 and 5:30 p.m. However, on one or two emigrations philovagans was found riding on larvae (2077, 2106-A), and on one occasion (2271-X) it rode on alate males of vagans (colony E-240), Thus, it appears that this species seldom if ever rides on workers, the queen, or booty but will ride on larvae when they become at least half grown. Limulodes philovagans runs along the trails much more slowly than the ants and also meanders to both sides of the trail. Since philovagans was found at the beginnings of emigrations even before the workers had started carrying the brood, such an early departure from the old bivouac may help prevent the limulodid's becoming lost. The only exception to an early emigration by Limulodes was one specimen taken at 7:10 p.m. along an emigration trail about two meters from a bivouac site shortly after all the workers had departed (colony E-141). No other species of Limulodidae was ever seen after the ants had completed emigrating at any point along a trail. The latter case and one other where there was a break in a column showed that at least this species of Limulodidae can follow the chemical trail when no army ants are on it.

Limulodes (*Carinolimulodes*) *brachyscelis* *Seevers and Dybas*: This species is known only from *E. burchelli* and is rare in colonies compared with *Cephaloplectus*. *L. brachyscelis* rides on larvae and also was found among young larval brood in laboratory nests.

Limulodes sp. 6: One specimen (2271-X) of *Limulodes* sp. 6 was found riding between the ocelli of an alate male of *E. vagans*. In the laboratory this *Limulodes* moved to the underside of the distal segment of the middle tarsus. The limulodid stayed there for about five minutes, being stepped on every time the male put its foot down. This specimen came off as I was trying to determine how it was holding onto the male. At least nine other individuals (2106-B) of this same species of *Limulodes* were found riding on the undersides of the distal and penultimate tarsomeres of the middle and hind legs of *vagans* workers. These limulodids are only slightly wider than the tarsus of the larger workers on which they were riding. Each specimen was oriented with its head at the base of the tarsomere, and the tip of its abdomen protruded a slight distance between the tarsal claws. In this position the tarsal claws did not touch the surface on which the ant was standing. The ant essentially walks on the dorsum of the limulodid. The one time when a limulodid was seen on the penultimate tarsomere another limulodid was already at the end of the tarsus. Because workers taken directly from an emigration column had the limulodids on their tarsi, this unusual location must be the most common natural position where the species rides. Except for an occasional brief stay on some other part of the leg or body of the queen or workers, this species of limulodid was almost constantly in this position. Although a queen was in the laboratory nest, and the limulodids shifted positions or moved to other ants from time to time, none ever got on the tarsi of the queen. In addition to licking the surface of the queen, *Limulodes* sp. 6 licked the surfaces of wet leaves and soil in preference to wet cotton.

Limulodes *spp*.: *Limulodes* sp. 3 (1876) and sp. 4 (1912) were taken from emigration columns of *L*. *praedator*, *Limulodes* sp. 5 (2075) (a new species near *tibialis* Bruch) was taken in an emigration column of *E*. *dulcius* *crassinode*, and *Limulodes* sp. 7 (1826) along with a new genus (1826) was taken from an emigration column of *Nomamyrmex* *esenbecki*. It is not known whether any of these species were running or riding.

Staphylinidae

In addition to over 7,000 specimens of Staphylinidae collected from refuse deposits, over 300 myrmecophilous specimens were taken on Barro Colorado Island from columns or bivouacs of army ants. These myrmecophiles belong to at least 27 species, and six additional species were taken with army ants in Kansas. I am indebted to Dr. C. H. Seevers for determining most of the specimens and describing some new species. Many of the determinations used here are tentative and may be changed when types can be examined. As larger series of a few species are now available for study, it is apparent that diagnostic characters previously used may no longer be valid for separating species. Unfortunately, most of the species were described from one or several specimens taken at a single locality. Approximately 80 genera and 180 species of Staphylinidae are known from Ecitonini. Borgmeier (1949) published a catalog of these species, and subsequent additions and corrections have been published by Borgmeier (1956, 1958b, 1959) and Seevers (1958, 1959). All the species taken in Panamá and Kansas during this study are listed below in alphabetical order under the most complete determinations available. The locations within colonies, host species and total number of specimens taken will be given for each species followed by notes on its behavior. Some field numbers will be given in parentheses in the discussions of the species to make it possible to connect observations with actual specimens. Unless some other data are given, all specimens listed below from ant columns refer to beetles seen running in or directly next to the columns, and all specimens were taken on Barro Colorado Island.

Dinocoryna tibialis Seevers: In raid and emigration columns of *Neivamyrmex opacithorax*, Lawrence, Kansas (2).

Dinocoryna tibialis and other species found with *Neivamyrmex* in the United States have been discussed taxonomically by Seevers (1959). His paper lists all the specimens found during this survey in Kansas.

Ecitochlamys sp.: In raid and emigration columns of *Nomamyrmex esenbecki crassicornis* (42).

One specimen of *Ecitochlamys* was taken as it was running along the chemical trail more than 30 minutes after the last ants had passed in a raid or emigration column of *Nomamyrmex esenbecki* (colony E-160). *Ecitochlamys* sp. was observed scraping and licking the surfaces of workers of *Nomamyrmex* in laboratory nests with its mandibles and other mouthparts. The beetle often started by cleaning one surface of an ant's leg, and then it pulled and turned the leg with its mandibles and cleaned the opposite side. Even though one or two beetles climbed around on the ant and appeared to bite the leg quite hard, the worker stood almost motionless. While licking the surfaces of the leg, the staphylinid intermittently rubbed the tip of its abdomen against the dorsal surfaces of its own elytra, prothorax and head. After the leg was thoroughly cleaned, the beetle went over the upper parts of the thorax and abdomen. Several workers were watched as they were cleaned in a similar manner, but the *Ecitochlamys* never attempted to clean an ant's front legs, any tarsi, mouthparts or ventral surface. The beetles did not concentrate at the joints between segments but went over the entire surface of a leg segment. Unlike the similar cleaning of *Nomamyrmex* done by *Zyras* sp., *Ecitochlamys* moved its mandibles constantly and extremely rapidly over the surface of an ant. The beetle usually went over a small area several times before moving on to a different spot. A limulodid, *Cephaloplectus* sp. (1814), rode on the abdomen on one *Ecitochlamys* in a laboratory nest but was not seen to clean or lick the staphylinid.

Ecitocleptis socia Borgmeier or n. sp.: In emigration column of *Noma*.*esenbecki* (3).

Ecitogaster n. sp.: In emigration and raid columns of *L. praedator* (12).

One specimen of *Ecitogaster* n. sp. (2262) was put in a laboratory nest with eight active and three inactive workers. The ants ignored the beetle which ran among them. Even after all workers were pinched to prevent them from possibly killing the beetle, the *Ecitogaster* ignored them.

?*Ecitomedon sp.*: Found in emigration column of *L. praedator* (1).

Ecitomorpha melonotica Mann: In bivouac sample, raid and emigration columns of *E. burchelli* (17).

Two specimens of *Ecitomorpha melonotica* (1404, 1408) were riding on cocoons.

Ecitomorpha nevermanni Reichensperger: Found in emigration columns and bivouacs of *E. burchelli* (19).

One specimen (1403) was found riding on a cocoon, and two specimens (1679) were riding on booty or hanging onto the workers carrying the booty. *Ecitomorpha nevermanni* resembles its host, *E. burchelli*, to a greater extent in color than in morphology (see figure 48). The legs and antennae of living specimens are the identical shade of brownish black. The abdomen is a dark amber brown, and the head and thorax are darker, matching the colors of many of the intermediate workers. Compared with the abdomens of generalized Staphylinidae, the abdomen of *Ecitomorpha* is morphologically more similar to those of the army ants. However, part of the similarity seems negated by the staphylinid's habit of holding the abdomen straight or slightly turned upward toward the tip. *Eciton* always holds the tip of its gaster close to the substrate on which it is running. The antennae of this staphylinid are similar to those of its host in length, thickness, position and virtually constant up and down vibration.

Two specimens of *E. nevermanni* (1679) were placed in a petri dish (20 cm. diameter) at 8:00 a.m. on the morning after they were taken from the emigration column. For the next four hours these staphylinids almost constantly rode on or cleaned two histerids, *Euxenister caroli* Reichensperger (1679), taken from the same emigration. *Ecitomorpha* used its legs to hold onto the large carinae on the dorsolateral angles of the thorax. Most frequently the staphylinids faced anteriorly, but sometimes they faced posteriorly or in other directions. At times an *Ecitomorpha nevermanni* remained in the same position on the histerid for more than ten minutes. At other times it frequently shifted position, intermittently cleaning or scraping the surface of the *Euxenister*. Three pieces of booty (larval and pupal ants from the emigration, and an adult polybiine wasp which I added) were in the dish but were ignored by the staphylinids. A large and a small intermediate worker were also ignored by both species of beetles. Six hours after the beetles and ants had been placed in the dish, a major worker was added. Within two minutes one Ecitomorpha started cleaning the tarsi of the major. The Euxenister climbed on the major and rubbed the ant's head with its legs (discussed more fully below in the section on Histeridae). While the histerid was rubbing the ant, the Ecitomorpha rode on the back of the histerid and rapidly shifted its position and rotated as the histerid constantly pushed aside the legs of the staphylinid. The major worker stood quietly while the beetles were running and rubbing on its head. When the Ecitomorpha was on the back of the histerid which was riding on the middle leg of a major worker, the ant walked without making any attempt to remove this large asymmetrical weight.

The Ecitomorpha apparently did not irritate the Euxenister since the histerid did not try to scrape the staphylinid off its back. However, the histerid probably could not reach above its own thorax with its legs. When the histerid was rubbing a worker with its legs and scraped one of the staphylinid's legs off the outside edge of the dorsolateral carinae, the staphylinid hooked another leg over a carina. The histerid never "played dead," retracting all its legs and antennae, but it constantly ran around while the staphylinids were on it. When the histerid ran under cotton which brushed the staphylinid off, the Ecitomorpha immediately followed the histerid and got on its back again.

While licking or cleaning the major workers, the Ecitomorpha did not use its mandibles but kept them spread widely. The staphylinids went over the legs of the ants more frequently and thoroughly than any other part of their bodies. Sometimes straddling the ant's leg, the staphylinid stood on the bottom of the dish and worked up and down on the dorsal surfaces of the ant's tibiae and tarsi. Sometimes the staphylinids climbed on a leg of the ant and cleaned part of the tibia or femur.

Usually the beetle went over the same small area of the leg several times before moving on to an adjacent area. In addition to licking the surfaces of the major worker and the histerids, *Ecitomorpha* drank water from cotton. During extensive observations throughout two days, this staphylinid never was seen to feed on the booty.

When touched by the ants or forceps, *Ecitomorpha nevermanni* was never attacked by the ants and never turned in small circles in the typical reaction of Thysanura, *Grassiella* spp. and *Trichatelura manni* (Caudell). This staphylinid never was seen to turn the tip of its abdomen up over its thorax, and probably it can move the tip of its abdomen upwards only slightly. There was no evidence that any repellent or attractive substance came out of the tip of the abdomen. The *Ecitomorpha* was frequently kicked on its back and had some difficulty righting itself apparently because its abdomen is not as mobile as that of *Tetradonia*.

Ecitomorpha sp.: In bivouac sample of *E. burchelli* (2).

Ecitonidia wheeleri Wasmann: In bivouacs of *Neiv. nigrescens*, Lawrence, Kansas (2).

Ecitonidia wheeleri can follow the chemical trails of its host.

Ecitophya bicolor Reichensperger: In emigration columns and in a refuse deposit (945-A) of *E. burchelli* (3).

A specimen of *Ecitophya bicolor* (137~~5~~3) was added to a dish containing the queen, workers, and other myrmecophiles from colony E-110. The *Ecitophya* immediately climbed on the back of a worker slightly larger than itself and started vibrating its mouthparts over the surfaces of

Corrections for Thesis (C. W. Rettenmeyer)

p. 471, last ¶, first line should read 1373 not 1375.

p. 471, second ¶ from bottom should read, "E... bicolor.... In emigration columns, bivouacs, and refuse deposit (945;A) of _E_. _burchelli_ (5).

the gaster, alinotum, vertex and parts of several legs. When the worker ran across the dish, the staphylinid got on a second worker and repeated the process. The *Ecitophya* also rubbed its legs alternately on the body of the worker and then on its own body. This rubbing was not as thorough as that seen performed by histerids. The *Ecitophya* ran over the queen several times but did noi stop to "clean" or rub its legs on her.

Ecitopora n. sp.: In bivouacs, refuse deposits and flying near bivouacs of *E. burchelli* (over 150).

This species was one of the most common staphylinids found in refuse deposits of *burchelli* where it feeds on remains of booty. *Ecitopora* must fly to new bivouacs because no specimens were ever taken along emigration columns, and flying specimens (1201) were common near bivouacs in the early evening as it became dark (5:30 to 6:30 p.m.). Some individuals landed immediately on leaves, but most flew back and forth a few centimeters above the refuse deposits for several minutes before landing. By 7:00 p.m. only an occasional specimen was seen flying and none was seen at dawn or later in the morning. Although *Ecitopora* was found in two bivouac samples, those samples included detritus from the periphery of the nests.

Labidoglobus nevermanni Reichensperger: In raid or emigration column of *L. praedator* (1).

Microdonia kansana Seevers: In bivouacs and emigration columns of *Neivamyrmex nigrescens* and *Neiv. opacithorax*, Lawrence, Kansas (41).

M. kansana ran in the center of emigration columns and could follow the chemical trails of the ants when workers were not on them. There was a slight increase in the numbers of this species at the end of an emigration.

Microdonia sulcatula (Borgmeier): In bivouacs and emigration columns of *Neiv. nigrescens* and *opacithorax*, Lawrence, Kansas (23).

The comments above under *M. kansana* apply also to *M. sulcatula*.

Mimeciton antennatum Mann: Found in raid or emigration column of *L. praedator* (16).

[illegible]

Mimeciton coeci Reichensperger: In raid column of *L. coecus* (1).

Mimonilla ?ecitonis Wasmann: Found in raid and emigration columns of *L. praedator* (7).

One specimen (1878) was being carried by a worker, and a second specimen (1879) was either being carried or more probably was riding on the worker which was carrying a histerid (*Convivister nevermanni* Reichensperger). *Mimonilla ecitonis* is entirely a light orange or straw color except for the tip of its abdomen which is brown. Although the abdomen is strikingly similar to the host's gaster in shape, the color of the staphylinid and position of the abdomen were noticeably different from those of the workers. The tip of the abdomen was always turned up when the staphylinid was seen in columns or in laboratory nests. This position, the darker color and the longer setae at the tip of the abdomen suggest that perhaps there are secretory glands there which produce some substance attractive to the workers. The workers frequently held *M. ecitonis* by the thorax and carried this species in laboratory nests as well as along columns.

Mimophites borgmeieri Reichensperger: Found in emigration column of *L. praedator* (1).

Mimophites tenellus Reichensperger or n. sp.: In raid or emigration columns of *L. praedator* (2).

Synecitonides phasma Reichensperger: In raid or emigration column of *L. praedator* (1).

Tetradonia marginalis Reichensperger: In refuse deposits and in raid and emigration columns of *E. burchelli*, in raid and emigration columns of *hamatum*, and in emigration columns of *vagans* (57).

Tetradonia marginalis was never found in a sample of ants taken from a bivouac, probably because this beetle stays around the periphery of the nests. It was seen throughout the emigrations of *hamatum* and *burchelli* and could readily follow the chemical trails of the ants when no ants were on them (876, 1625, 1658, 1964). On two occasions this species was found on trails more than 20 minutes after the last ants were seen on them. However, this staphylinid was probably most common at the beginning of emigrations. It was the beetle most frequently seen along raid columns and along those columns changing from raid to emigration columns. *T. marginalis* appeared to avoid the center of a column of *burchelli* more than the center of a column of *hamatum* (1388, 1389). If this difference did not occur by chance, it may have been due to the less dense columns of *hamatum* and the fact that *hamatum* does not attack as readily as *burchelli*. *T. marginalis* was one of the few myrmecophiles found in raid columns during the day (2221).

Tetradonia marginalis was the species seen most frequently attacking apparently uninjured, active workers as well as injured workers along the edges of columns and near bivouacs (923, 962, 1625, 1693). The staphylinids were not seen to attack workers running along in the middle of raid or emigration columns or those running quickly along the edges. Workers either standing still or walking slowly along the edges of columns were attacked. After one staphylinid started an attack on a worker, a second beetle coming along the column would often join in the battle. _T. marginalis_ also carried dead workers away from refuse deposits where they had been dropped by the army ants.

When attacking an active worker, _T. marginalis_ distinctly avoided the anterior end and first attacked the posterior or middle legs of the ant. Rushing at the ant, it grasped the ant's leg in its mandibles. When the ant wheeled around to face the staphylinid, the beetle apparently shot an invisible gas or liquid from the tip of its abdomen directly toward the head of the ant. This substance seemed to stun the ant. While the ant momentarily paused, the beetle had time to circle to the opposite side and again bite or pull at the ant's leg. After a worker had been "gassed" about five times, it no longer wheeled or ran toward the staphylinid and soon could no longer stand. There was no indication that the legs of the workers had been injured by the staphylinids until after the ants could no longer stand up. Several times workers were put with one or several of these beetles in petri dishes covered with sheets of glass. Little air entered these dishes, and it appeared that all the workers became weakened or killed by a substance from the beetles even though each ant was not attacked directly.

When more than one beetle attacked the same ant, it first appeared that the beetles were co-operating. At first both beetles pulled the hind legs of a worker or alternated the pulling with the chemical attacks.

However, after the ant was overpowered, the staphylinids often grabbed legs or antennae at opposite ends of the ant and sometimes spent over an hour pulling the ant first one way and then another. A single staphylinid sometimes carried a dead worker held over its head, but more often the beetles pulled the ant 50 to 250 cm. away from the bivouac and then proceeded to cut the ant apart. Two staphylinids had much more difficulty feeding than a single individual since one of them usually started pulling the ant away. Occasionally three or four beetles pulled on the same worker. Even single beetles sometimes pulled an ant for about 15 minutes in one direction and then pulled it in the opposite direction.

It is not known whether _T. marginalis_ ever oviposits on or buries the workers. It did not seem to be able to eat much of the ants but did cut them apart at the joints. The appendages were usually trimmed off first and then the three main regions of the body were separated. Legs were removed at the bases, or the tibiae or femora were removed. The staphylinids frequently abandoned the workers without dismembering them completely. The beetles clearly fed on the juices coming from the open ends of the sclerotized pieces but were not seen to cut any of the heavily sclerotized areas. Perhaps the prey is partially digested outside the bodies of the beetles, and the staphylinids ingest only liquids as was suggested by the fluid which sometimes was seen around the mouthparts of the feeding beetles.

Tetradonia prosequens Reichensperger: In raid and emigration columns of _E. hamatum_ (ca. 80).

T. prosequens was found in all parts of emigrations as well as after all the ants had emigrated, and it ran in the center of the columns rather than along the edges. This beetle was found on Barro Colorado Island only with *hamatum*, in contrast to *T. marginalis* which was found with three species of *Eciton* including *hamatum*. In Costa Rica *T. prosequens* was also found only with *hamatum*, but *marginalis* was found with *burchelli* and *hamatum* (Reichensperger, 1935: 215-216). *Tetradonia prosequens* also was observed capturing adult ants as shown in figure 43. However, *prosequens* appeared less aggressive than *marginalis*. It also fed on material scraped and licked from the surfaces of dead workers. One individual (1529) taken from an emigration column (colony E-121) on 18 March 1956 lived until 29 or 30 March. During this period it was in a petri dish (diameter of 8 cm.) with one major and six intermediate workers, young larval brood and booty from its host colony, and water. At no time was the staphylinid seen feeding on the booty or brood. The workers died so gradually that it is unlikely that the *prosequens* killed them. Three workers were still alive on 23 March, and one was alive after the staphylinid died. The staphylinid piled the dead workers at one side of the dish next to a ball of moist cotton and frequently hid in the pile of dead workers where it appeared to feed on the surfaces of their bodies but did not cut them apart.

T. prosequens has a strong odor which is more likely repellent or injurious to the workers than attractive to them. The workers of *hamatum* several times bit at *prosequens* in laboratory nests but did not do visible damage. One *prosequens* was kept in a petri dish (15 cm. diameter) with about 150 workers from its host colony of *hamatum* (E-162). After three and one-half days all the workers except for four majors were dead. This mortality may have been largely or entirely due to starvation. However, even though the cover of the dish had been removed several times after the ants and myrmecophile had been placed in it, the odor of the beetle was immediately noticed. No odor of the *hamatum* could be detected due to the strong odor of the *prosequens*.

Tetradonia n. sp.: In raid and emigration columns of *E. vagans*, *dulcius crassinode* and *mexicanum* (10).

This species of *Tetradonia* (1597) was seen to go over the surfaces of dead workers with its mouthparts, but it was not seen to attack living workers. The dead workers were dragged by the staphylinid to a refuse deposit made by workers of *dulcius* fed in a laboratory nest with *Polistes* brood. This *Tetradonia* was never seen to feed on the booty refuse. The longest any specimen survived in a small laboratory nest was seven days.

Vatesus lucidus Mann: In raid column of *Neiv. gibbatus* Borgmeier at about 4:00 a.m. (1).

Vatesus panamensis Mann: In bivouacs or emigration columns of *E. burchelli*, *hamatum*, *vagans*, *dulcius crassinode* and possibly *mexicanum* (82 adults, 59 larvae and 1 pupa reared from a larva).

V. panamensis was considered a synonym of *clypeatus* Wasmann (Seevers, 1958: 188), but there is still some doubt whether this is a correct interpretation. Since Barro Colorado Island is the type locality for *panamensis*, additional specimens collected there are more likely conspecific with that species than with *clypeatus* which was found in Brasil.

V. panamensis was usually taken during the central parts of emigrations while the brood was being transported. It runs in the middle of the column and is apparently ignored by the ants (see figure 54). Holmgren (1908: 344) reported that when *Vatesus goeldi* (Wasmann) was following the columns of its host, the beetle hurried forward from hiding place to hiding place. It would often get in the way of the ants and then would hide under a leaf. No species of *Vatesus* observed in Panamá hid under leaves or other objects while it was emigrating unless I touched the beetle when attempting to pick it up. If an ant stepped on a *Vatesus*, the beetle sometimes went to the edge of the column but continued its progress. No specimen was ever seen riding on workers, queens or males, and it is doubtful whether this species of *Vatesus* could easily ride because of its large size. On one occasion *V. panamensis* (2170) was seen running in an emigration about 30 cm. behind a queen of *E. vagans* but within the retinue of workers accompanying her. Most other myrmecophiles were not seen running in retinues of queens possibly because of the greater excitement among the workers there. *V. panamensis* was never seen in raid columns except for one case when colony E-189 (*hamatum*) omitted an emigration in a nomadic phase. The beetle ran a short distance out along the raid column at 6:40 p.m. and returned to the bivouac.

A few specimens of *Vatesus panamensis* were seen in bivouacs, and these were in the areas containing the larval brood. On two occasions at night I saw this species leave a bivouac of *burchelli* and run along a refuse column to the refuse deposit where the beetle fed on remains of the army ant booty. In laboratory nests it also fed on booty and on fluids from larvae of *burchelli* which had previously been pierced by a histerid. Most specimens of *Vatesus panamensis* ran around almost constantly when placed in laboratory nests. They avoided light and crawled into any corners or cracks where it was darker than the main nest. Without such hiding places they appeared to become exhausted and died in a few hours. This staphylinid never was seen to feed on the surfaces of the ants and avoided all possible contact with the workers. On one occasion a specimen climbed on a queen (*E. vagans*) but not for more than a few seconds. Several times *V. panamensis* was seen to rest while touching other specimens of its species, but it would not rest in the same way in a group of workers.

When a worker ant stepped on the top of these staphylinids, the beetles did not raise the tips of their abdomens like the predatory *Tetradonia*. Repeatedly when a worker ran over or attempted to bite *V. panamensis*, the staphylinid pulled its antennae, but not its legs, under its large pronotum, stayed motionless for two or three seconds and then ran off. When these beetles died in laboratory nests, sometimes the ants pulled them partially apart; and sometimes, even when there had been no food in the small nests for up to nine hours, the ants ignored the beetles. One active *Vatesus* (1232) was promptly killed and eaten in a laboratory nest containing several thousand *burchelli* workers from its host colony.

V. panamensis ignored myrmecophilous Thysanura, Histeridae, and other genera of Staphylinidae; all of which likewise ignored the *Vatesus*. However, a limulodid, *Cephaloplectus* (1354), was seen to "clean" a *Vatesus* in the same manner in which it licked and scraped over the surfaces of the ants. While the limulodid was rapidly going over the dorsal surface of the male *V. panamensis* (1376), the staphylinid shook back and forth until the limulodid was dislodged. (A more detailed observation of comparable behavior is given below under *V. rettenmeyeri*.)

Over 70 larvae of *V. panamensis* were taken in emigration columns of *Eciton* spp. on Barro Colorado Island. Their identification seems certain because: (1) they belong to the subfamily Tachyporinae (det.

Seevers) which includes no other genus found with Ecitonini; (2) the larvae are larger than most or all other staphylinids found in these colonies; (3) no other species of Vatesus is known from most of the hosts; and (4) one specimen was reared from a larva to a pupa having the main morphological features of Vatesus. I believe these are the first larvae which have been identified for any species of myrmecophile found with the army ants. Only one other much smaller species of unidentified staphylinid larva was found running in an emigration column of army ants in Panamá.

The Vatesus larvae were taken from emigration columns of two colonies of hamatum (E-121 and E-168) and one colony of E. dulcius crassinode (E-137). Since both panamensis and a similar species of Vatesus were taken with dulcius crassinode, the last group of larvae may belong to either species. One larva of panamensis was taken at about 8:00 p.m. along a raid column on the 21st and last statary day of colony E-168. At this time several Tetradonia and two Thysanura, Trichatelura manni (Caudell), were also seen in the raid column. These myrmecophiles were running both away from and toward the bivouac. However, those going away from the bivouac were sometimes forced to reverse their direction since at least 95% of the ants were running toward the bivouac. Any possibility for an emigration apparently was blocked by this incoming traffic, and all the myrmecophiles probably would have returned to the bivouac. Except for the above case, all larvae of Vatesus panamensis taken with hamatum were found during two emigrations beginning nomadic phases. Most of the larvae were at least three-fourths grown, and some became inactive prepupae within three days of when they were taken. Therefore, it is probable that eggs or larvae are deposited by the adults in the bivouacs near the beginning of the statary phase. The above evidence is the best yet found to support the hypothesis that some myrmecophiles have a life cycle correlated with the life cycle or activity cycle of their hosts.

The larvae were more highly restricted in the time when they emigrated than any other group of myrmecophiles seen running in the columns. For example, in the emigration of colony E-121 on 18 March 1956 at least 80% of the ants were running away from the old bivouac at 5:00 p.m., and the first booty was seen being carried away from the bivouac at 5:27 p.m. At 6:23 p.m. one larval Vatesus emigrated. The emigration gradually became stronger with numerous callow workers in the column by about 7:00 p.m. and with young brood primarily carried between 7:30 and 8:30 p.m. Seven adult V. panamensis were taken between 7:27 and 8:34 p.m. After 9:00 p.m. the column gradually decreased until the last workers passed about 9:20 p.m. The second Vatesus larva was seen in the column at 9:10 p.m., three more were seen between 9:21 and 9:23 p.m., and 14 were seen between 9:24 and 9:26 p.m.

On 13 June 1956 a first nomadic emigration of a second colony of hamatum (E-168) also had the larval Vatesus only at the end. Between 6:15 and 6:50 p.m. the emigration route was followed to the new bivouac which was judged to contain about ten per cent of the colony at 8:40 p.m. Larvae of Vatesus were not seen along the column when it was followed, nor were they seen from 6:50 until 9:15 p.m. while the column was watched constantly. Four larvae passed between 9:15 and 9:30 p.m., ten between 9:30 and 9:45 p.m., and 15 between 9:45 and 9:52 p.m. Only a few ants were in the column after 9:30, and the last worker was seen at 9:51 p.m. Although the trail was watched until 10:27 p.m., no more larvae of Vatesus were seen along it.

The third emigration which included larval *Vatesus* was that of *E. dulcius crassinode* (colony E-137) seen on 2 April 1956. This emigration probably was the first one in a nomadic phase since numerous light callows, a few cocoons containing *dulcius* workers, and numerous eggs and young larvae were in the column. No larval *Vatesus* were seen until 16 ran along the route just before and after the last workers were passing the observation point.

In conclusion, virtually all larvae of *Vatesus* emigrate in the final few meters of an emigration column. A few may emigrate at the beginning of emigrations. The adults, however, emigrate primarily in the middle of the emigration while brood is being carried. Although no larval *Vatesus* were seen in a bivouac, these data suggest that the larvae are found in the bottom of the bivouac rather than among the brood. Perhaps they feed on booty or booty refuse which is more concentrated near the bottoms of bivouacs.

Unlike the millipeds, the larvae of *Vatesus* do not become more abundant at the end of an emigration as a result of their running more slowly than the ants. Not only did they appear to run just as quickly, but one emigration of *hamatum* was watched one to three meters from the old bivouac, too close for any difference in rate of running to be significant. Moreover, the larval *Vatesus* were also at the end of an emigration watched ten meters from the old bivouac. The larvae did not appear to be bothered by the workers running on top of or next to them. No larva was carried by a worker. In laboratory nests the workers and larval *Vatesus* ignored each other except for one occasion when four workers simultaneously attacked a larva. No visible damage was done to the larva, and the workers ceased the attack after a few weak bites. The long setae protruding from all sides may provide some protection. When the head is retracted it is covered by a large pronotum as in figure 50. If workers ran over a larva or if the anterior end was grasped with forceps, the larva held onto glass or other substrates by the pygopod on the tip of the abdomen (see figure 50). The larvae did not feed on booty or the eggs and young larvae of *hamatum* but did feed on injured worker prepupae of *burchelli* put in the laboratory nest. Several phorids were also killed and eaten by larvae of *V. panamensis* in a vial. The lack of feeding by most of the larvae may be attributable to their being ready to pupate.

One larva taken on 19 March became a prepupa on 22 March and a pupa on 26 March. Photographs of these three stages are shown in figures 50 to 53. The larva does not molt when changing to a prepupa. As can be seen in figure 52, the body of the prepupa is curved with the head and legs drawn close together. All the prepupae lay on their sides in this position. Although one prepupa molted to a pupa in three days, other prepupae were kept for as long as ten days without molting. None of these appeared dead or injured within that period. No movement could be detected in any of the prepupae which were handled with forceps, but the pupa moved slightly. On the day after the prepupa molted, acarid mites were found feeding on the pupa, and on the following day the pupa was preserved because of the damage being caused by the mites in spite of attempts to remove them. All other larvae and prepupae died within ten days.

Since no prepupae nor pupae were found in columns, they may be found in detritus of soil beneath the bivouacs. (No dirt was in the laboratory nests.) The adults have wings and could fly to new colonies after emerging. It would be unlikely that wings would be retained by these otherwise highly modified beetles unless they were of adaptive value. The beetles were never seen to fly even when picked up and dropped a distance of about one meter.

Vatesus praedatorius Seevers: In raid columns of three colonies of L. praedator (15).

These beetles were all found running in the centers of raid columns during the day and night (approximate times: 5:00 and 8:00 a.m., 2:00 and 9:00 p.m.). The largest number taken with one colony was nine found just behind the swarm front. One beetle (with five workers) and two beetles (with 15 workers) were alive in vials two hours after they were collected but were dead seven hours later. The dead specimens showed no damage caused by the workers. Water but no food had been provided during this period. This species has also been taken with L. praedator in Costa Rica (Seevers, 1958: 196).

Vatesus rettenmeyeri Seevers: In emigration column of Nomamyrmex esenbecki crassicornis (colony E-164) (82 seen, 70 taken).

Vatesus rettenmeyeri was found running in the center of the column during the middle of an emigration when brood was being carried. In contrast, V. schneirlai was found with the same colony but only in a raid column and at the end of the emigration (see below). V. rettenmeyeri, like V. panamensis, did not seem to be attracted to booty, living or dead workers, or queens. Several times limulodid beetles (Cephaloplectus sp.) climbed on the backs of this staphylinid and started to "clean" them. Usually they fell or were knocked off the Vatesus within a few seconds. One Cephaloplectus (1821) rode on the pronotum of V. rettenmeyeri for about one minute. The *Vatesus* got highly excited and ran in tight circles twisting and turning rapidly while running around inside the nest. The limulodid moved down onto the abdomen and was shaken off when the *Vatesus* flipped its abdomen back and forth. Since the *Vatesus* immediately became quiet as soon as it was free of the limulodid, I believe the *Cephaloplectus* caused the violent activity. The response of the *Vatesus* was surprising since the pronotum and elytra appear to be heavily armored. Perhaps the limulodid grasped or pulled the scattered minute hairs on the dorsal surface of the *Vatesus*.

Vatesus schneirlai Seevers: In refuse deposit of *E. burchelli* and in a raid and emigration column of *Nomamyrmex esenbecki crassicornis* (colony E-164) (11).

A single specimen of *V. schneirlai* taken on 28 March 1956 was the only *Vatesus* found in about 100 samples from refuse deposits of *E. burchelli*. This sample was collected at 6:50 p.m. when *Vatesus* from the bivouac may have been visiting the refuse deposit. Two specimens were taken as they were running in a raid column of colony E-164 between 1:00 and 10:00 a.m. on 18 May 1956. During the evening and night of the same day this colony emigrated, but not a single *V. schneirlai* was seen. However, 82 *V. rettenmeyeri* were seen in the emigration column during the period of observation from 6:10 to 11:30 p.m. On the following day (19 May) when the emigration had almost ended, six more *schneirlai* were taken between 2:30 and 3:00 p.m. These data suggest that *Vatesus schneirlai* may stay around the edges of the bivouacs and may feed on the booty refuse deposited there.

Vatesus n. sp.: In emigration columns of *E. dulcius crassinode* (15).

Two of three emigrations of *E. dulcius crassinode* (colonies E-137, E-143 and E-204) included specimens of *Vatesus panamensis* in addition to this new species. The two species were both running in the columns with neither species being segregated at the ends of the emigrations as was reported above when *V. rettenmeyeri* and *schneirlai* were found in the same emigration.

?*Zyras sens. lat.*: In raid and emigration columns of *E. burchelli*, *hamatum*, *L. praedator*, *Noma. esenbecki* and *Neiv. pilosus*; in bivouacs of *burchelli* and *vagans*; and in refuse deposits of *burchelli* (about 65).

Several species of Myrmedoniini are grouped here since it is impractical to separate them at the present time. Some or all of these species feed on booty refuse and on dead army ants (1006), and a few species attack living workers. In the evening and early morning (unlike *Ecitopora*) these beetles fly around the bivouacs in large numbers (about 50 in a cubic volume about 30 cm. on a side) (1205, 1207). One specimen (2233) was taken over a swarm raid of *E. burchelli*. At least several species of ?*Zyras s. lat.* ran primarily along the margins of emigration columns rather than in the centers of the columns. These beetles were watched as they ran for several meters without attacking any workers.

Two specimens of one species (2132, shown in figures 45, 46, 47 and 49) were taken from a raid or emigration column of *Nomamyrmex esenbecki* and placed with a few workers in a petri dish. Regardless of whether it was attacking or feeding on an ant, this species of staphylinid almost constantly had its abdomen turned far up over its head (see figures 45 and 46). There was no clear indication that the ants were repelled by any substance coming from the tip of the abdomen. The beetles were not seen to attack each other or the active workers in the dish, but all the workers were almost dead within four hours. When an ant was still able to move but unable to stand, the staphylinids started dragging it around the dish. The beetles shifted their hold on the ants frequently even though the ants were not actively opposing them. Sometimes one beetle started pulling the leg of the other staphylinid, but it immediately ceased although the beetle being pulled did not retaliate but continued to feed or pull on the ant. Even when feeding on the same coxa or trochanter and also at all other times, the two staphylinids ignored each other. The beetles made no attempt to fly when one crawled on my hand or when the dish was not covered.

The beetles appeared to have two distinct methods of feeding. The first method was that used by most myrmecophilous staphylinids in which the mouthparts rapidly move back and forth, and the beetle seems to lick and scrape material from the surfaces of the ants. Fine particles on the ants could be seen to disappear as these staphylinids went over the ants with their mouthparts. These staphylinids (2132) also frequently cleaned their antennae and sometimes other parts of their bodies in a similar manner. In this method of feeding the mouthparts appear dry, and the mandibles are not used extensively if at all.

In the second method of feeding, the staphylinid grasped part of the ant with its mandibles, and a drop of fluid covered the mouthparts and area of the prey around the mandibles. The beetle then drew in the fluid except for a trace which often remained on the ant. The latter method was only used on the basal parts of appendages (pedicels, coxae and trochanters). No appendages or other parts were cut or pulled off the workers until about a day later.

Nine days after the staphylinids were taken, one beetle was found dead and being carried throughout the nest by the other. The legs and head had been removed from the dead staphylinid. On the previous afternoon both beetles had been active. Since no workers of *Nomamyrmex* were available, a worker of *Eciton* vagans was pinched to insure that it would not kill the staphylinid, and it was added to the nest. The staphylinid ignored the *vagans* completely.

New genus and species: In raid or emigration column of *Nomamyrmex esenbecki* (1).

Larvae, ?*genus*: In raid column of *Neivamyrmex humilis* (Borgmeier) (2).

These larvae (1297, 2198) were running in the raid column between 11:00 and 11:30 p.m. The subfamily could not be determined by Dr. Seevers.

Pselaphidae

The family Pselaphidae includes many myrmecophiles, and the species most highly specialized for living within ant colonies are in the subfamily Clavigerinae (Jeannel, 1956; Park, 1942). This subfamily, however, includes no species living with the African driver or American army ants (Dorylinae) (Jeannel, 1956: 198). Probably all myrmecophilous pselaphids, except for some of the clavigerines, are tolerated scavengers (synoeketes). However, on the basis of this limited survey in Panamá, it seems doubtful whether any Pselaphidae live within colonies of army ants (Ecitonini) even as tolerated scavengers. Nevertheless, three species have been reported associated with army ants, *Hamotus* (*Hamotoides*) *ecitophilus* Raffray, *Arthmius macrocephalus* Schaufuss, and *Decarthron euspinifrons* Park. The first species was found with large ants of the genus *Eciton* [*sens. lat.*] (Raffray, 1909: 47), and the second one was found in columns of *Labidus praedator* (Wasmann, 1900: 250). It was not stated whether the latter species was running, riding or being carried in the columns. The third species, *D. euspinifrons*, was taken on Barro Colorado Island with a quart of *Eciton burchelli* from a bivouac in a narrow interbuttress space. It was considered a synoekete of *burchelli* largely because it "was in the midst of a long festoon of ants and certainly would be quickly destroyed unless it was a tolerated guest" (Park, 1942: 197). Since no further specimens of this species were found in our survey of over a half million ants from more than 20 colonies of *E. burchelli* from the type locality, it seems improbable that *D. euspinifrons* is an ecitophile. Probably this species was found when the preserved ants were sorted. It may have been booty which sometimes remains intact for a time within a bivouac, or it may have been around the periphery of the bivouac.

Moreover, no specimens of Pselaphidae were found in samples of army ants taken from bivouacs, and no pselaphids were found in columns. Five species were taken in refuse deposits of E. burchelli, but these species were rare. Two of the species were found more frequently in forest floor litter where no army ants were seen. Until observations on the behavior of these beetles indicate that the species are clearly myrmecophiles, I believe all pselaphids taken near army ants have been found by chance and should be considered myrmecocoles.

Histeridae

About 140 specimens of Histeridae belonging to species which are distinctly myrmecophilous were collected on Barro Colorado Island. This total does not include about 185 specimens found in refuse deposits. In the latter group there are some species which may be myrmecophiles in the strict sense since they have also been found in samples from bivouacs of army ants. The discussion below will emphasize those species known to be myrmecophiles. All determinations have been made by Mr. Rupert L. Wenzel whose help and encouragement I wish to acknowledge. All the records listed are from Barro Colorado Island except where other data ~~is~~ are given. Specimens collected from columns may have been running, riding, or carried by the ants, if no specific details are given.

Alloiodites n. sp.: This species is primarily found in refuse deposits; however, one specimen (1876) was aspirated along with ants from an emigration column of *Labidus praedator* (colony E-177).

Cheilister lucidulus Reichensperger: In refuse deposit column of *Eciton burchelli* (1694) (1 sex?); in bivouac sample of *burchelli*, colony '55 B-IV-N (1040) (1 sex?).

Although *Cheilister lucidulus* was rare on Barro Colorado Island and never found in a column of *burchelli foreli*, it has been reported "in almost all columns" of *E. burchelli* at Hamburg Farm, Costa Rica (Reichensperger, 1935: 209-210). Borgmeier (1955: 188-189) stated that both *burchelli foreli* and *b. parvispinum* are found at Hamburg Farm near San José, Costa Rica. Reichensperger also reported that *Ch. lucidulus* had not been found in the mountains with *burchelli infumatum*, considered a synonym of *b. parvispinum* by Borgmeier. Therefore, the association of abundance of this guest with the subspecies of host does not appear to be as good as has been reported. *Cheilister monotonus* Reichensperger and *Ch. sphaeroides* Reichensperger, known from *E. hamatum* and *Neivamyrmex pilosus* in Costa Rica, have not been found on Barro Colorado Island.

Clientister henrici Reichensperger: In bivouac samples of *E. burchelli*: 17 March 1955, colony '55 B-IV-N (1040-A) (1 sex?); 20 April 1956, colony E-149 (1663) (1 sex?).

This species was originally described from several specimens taken with *burchelli foreli* in Costa Rica (Reichensperger, 1935: 190-193).

Convivister nevermanni Reichensperger: In emigration column of *L. praedator*: 30 May 1956, colony E-177 (1879) (1♂).

Convivister nevermanni was described from one specimen seen carried by a worker in a column of *L. praedator* at Hamburg Farm, Costa Rica (Reichensperger, 1936: 224-226; 1939b: 300). In Panamá one specimen was seen being carried in an emigration column by a worker; and when the worker was aspirated from the column, a specimen of *Mimonilla ecitonis* Wasmann was also taken. Apparently this staphylinid was riding on the same worker or on the histerid carried by the worker. During brief observations in a laboratory nest, a worker held and carried the histerid for about two minutes with its mandibles against the edges of the histerid's thorax. Since the *convivister* was carried dorsal side up, there is no possibility that it was holding onto the ant. The ants were not seen to lick this histerid.

Ecclisister bickhardti costae-ricae Reichensperger: In emigration columns of E. burchelli: 4 March 1955, colony '55 B-IV (954-B) (1 sex?), 8 March 1955, colony '55 B-IV (989-B) (1 sex?), 5 March 1956, colony E-110 (1356) (1 sex?); in refuse deposit of burchelli: 16 March 1955, colony '55 B-IV-S (1030) (1 sex?); in bivouac sample of burchelli: 20 May 1956, colony E-148 (1836) (2 sex?).

Ecclisister bickhardti (Reichensperger, 1923b: 248-249) was originally described from specimens found from burchelli in Brasil. The "subspecies" costae-ricae was described from specimens found in a column and nest of burchelli foreli at Hamburg Farm, Costa Rica. On Barro Colorado Island one specimen (1356) was found riding on the posterior end of a worker cocoon of burchelli being carried by an ant on an emigration starting a nomadic phase. A second specimen (954-B) was either riding on a male burchelli or possibly riding or being carried by a worker. A third specimen was riding on a male burchelli in an emigration. Later in a laboratory nest the histerid stood on the head of a male with its mouthparts close to those of the male. No fluid could be seen around the mouthparts of either insect, and it is not known whether the histerid was feeding.

Euxenister caroli Reichensperger: In emigration columns of E. burchelli: 23 February to 28 April 1956, colonies E-110, E-111, E-132, E-136 (4♂, 6♀).

All specimens of Euxenister caroli were seen in emigration columns of burchelli during the period when the army ant brood was being carried. At least 20 additional specimens were seen in columns and not taken. Six out of the ten specimens taken were running along in the center of emigration columns. The remaining four specimens were hanging onto a larva or cocoons carried by the workers. At least one of these histerids had one or two legs hooked onto the worker. However, it was clear from both field and laboratory observations that the histerids primarily hold onto the object carried rather than to the ants themselves. Laboratory observations indicated that these histerids climbed onto a cocoon or larva after it had been picked up by the ant rather than before it was picked up. The Euxenister rode on larvae and cocoons, either booty or brood. Euxenister caroli was seen on a number of other emigrations but was never seen along raid columns or in refuse deposits. Since these beetles run into the bivouac during the emigration, they undoubtedly stay within the temporary nest until the next emigration. This species probably runs more frequently during emigrations at the beginning of the nomadic phase after all the workers have emerged from cocoons but before the larvae are large enough for them to grasp.

Euxenister caroli has exceptionally long legs for a histerid (see figure 55), and it runs along the emigrations at approximately the same speed as the ants. This histerid appears quite awkward and is one of the most conspicuous guests found in the emigrations of burchelli. The elongation of the legs is probably partially an adaptation for increasing the speed of the histerid. When holding onto workers or other objects, the legs are sometimes folded tightly against the histerid's body with only the tarsi extended and grasping the object. This position of the legs was used when Euxenister caroli was seen riding on the underside of the alitrunk of a submajor worker. The posterior end of the abdomen of the histerid was directly below the anterior edge of the ant's gaster. Although the histerid appeared to be holding onto the middle and hind coxae, the ant still ran at full speed throughout the nest.

Euxenister caroli was frequently seen using its long legs for rubbing itself and the bodies of the ants. Usually it rubbed major workers, but occasionally it was seen on submajors or large intermediates. When two contracted queens (E-110 and E-136) were in dishes with workers, Euxenister was more attracted to major workers than to queens. The rubbing usually started shortly after Euxenister climbed on the thorax or head of a worker. The histerid rubbed two or three of its legs alternately at lightning speed for three to ten strokes against the alinotum and head of a worker. Then it rubbed the legs against the sides of its own body for several strokes. While rubbing with its legs, Euxenister folds its tarsi into grooves. Sometimes the histerid held onto the worker only by grasping a scape in its mandibles and then used four or six legs for rubbing the worker's head, antennae and mandibles. While two or three legs were rubbing extremely rapidly, the other legs shifted their position and did a little rubbing much more slowly. The rubbing continued for a few seconds even when the pair rolled over so that the histerid was lying upside down with the worker between its legs.

Sometimes the histerid moved to the ventral side of the head of a major worker and rubbed the ant's antennae and mandibles thoroughly. While rubbing the head, the histerid simultaneously cleaned the antennae with its mouthparts. It did not grasp the antennae with its mandibles but licked the surface or strigulated over it repeatedly with its maxillae.[1] The head of one major was rubbed almost constantly for four

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[1] The term "licking" is used here to indicate when an insect touches a surface with any of its mouthparts except the mandibles. The term

minutes at the same time that another *Euxenister caroli* rubbed it on the opposite side for two minutes. Through the entire process, the major stood almost motionless. When the histerid rubbed the more distal parts of the antennae or mandibles of a major, the hind legs were used to hold onto the major's head. The front and middle legs were used alternately or simultaneously for rubbing. When *Euxenister* used its front legs for rubbing ants, it also rubbed the top of its head with these legs.

The frequency and duration of this rubbing by the histerid suggests that it has some biological importance. Perhaps by this process the *Euxenister* transfers the ~~chemical~~ colony odor from the surface of the ants to its own body. The beetle can rub its legs on all exposed surfaces of its body except the pronotum and the part of the elytra between the dorsolateral carinae. Therefore, the beetle could transfer the odor from the ants to the parts of its body most subject to attack or injury by the ants. When army ants become maximally excited while attacking an insect, they sometimes grasp the leg of another worker in their mandibles but immediately release it. Presumably the same chemical which protects the workers from being injured by members of their own colony also protects the histerids. Reichensperger (1924a: 130-131) reported that histological sections showed that the prothorax of *Euxenister* is filled with masses of glands which discharge through pores on the outer surface, and the long yellow hairs on the prothorax and elytra have been considered "trichomes" presumably highly attractive to the ants

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"strigilating" indicates a rapid scraping by the mouthparts. The maxillae are used most extensively in strigilating, but some insects use other mouthparts including the mandibles. The mouthparts usually move more slowly when licking than when strigilating.

(Reichensperger, 1923a: 334). A detailed study of the histology of *Chrysetaerius iheringi* Reichensperger showed that a unicellular gland opens in the socket of each trichome hair and apparently secretes an oil which covers the hair (Seyfried, 1928: 26). The glands of *Euxenister* may be similar; and because the ants were never seen to lick or be attracted to the trichomes, the possibility exists that the main function of the oily secretion is to absorb material from the surfaces of the ants. The trichomes on the dorsolateral carinae may be more important for rubbing material off of the histerid's legs rather than for holding the glandular secretions in a place where the ants can readily lick them. It would seem less likely that the histerid uses its legs to transfer the oily secretion from the dorsolateral trichomes to the bodies of the ants. The long hairs on the inner surfaces of all the tibiae are most likely adaptations for increasing the efficiency of the rubbing process. Seyfried (1928: 21-22, 27, 57) thought that the long hairs on the legs of *Chrysetaerius iheringi* were covered with a secretion which "charms," "pleases" or "fascinates" the ants and thus protects the legs. However, the hairs on the legs of *Chrysetaerius* are also most extensively developed on the *inner* surfaces of the middle and hind tibiae. If these hairs on the legs of both genera have a protective function, one would expect to find the hairs on the *outer* surfaces of the legs. In addition, there was no direct evidence that the ants were attracted or repelled by any substance on the legs or dorsolateral trichomes of *Euxenister* when the ants bit them. The possibility remains that the long hairs are of some protective advantage because they sometimes pull out or break off when an ant bites them and thus may allow the histerid to escape. Such attacks may be frequent in nature because specimens of different genera of histerids have been found with many hairs missing. These histerids have been considered grazed upon ("abgeweidet," Borgmeier, 1948b: 390) by the ants because the hairs were assumed to be covered by a highly attractive substance. However, the only times ants licked Euxenister caroli were several periods of one or a few seconds when they licked the outer surface of a leg. The most highly attractive substance from caroli appeared to be its fecal material. When one beetle defecated a drop of white fluid on a piece of glass, three workers immediately were attracted to the drop and licked it up within a few seconds.

Some inconclusive evidence supports the hypothesis that the rubbing by the histerids decreases the vigor of attacks by the workers. One male and one female Euxenister caroli (1235, 1236) were taken from an emigration on 23 February 1956 at about 8:00 p.m. These histerids were kept isolated from all other insects until they were introduced into a laboratory nest 16.5 hours later. The ants in this nest were from the same colony, but they had been taken on 20 February. No histerids were in the laboratory nest until the two Euxenister were introduced. As soon as the histerids were put in the nest, they were attacked by several workers. When attacked by workers or touched by forceps, Euxenister did not wheel around as Thysanura do but stood quietly or ran off. If touched hard enough by forceps, the beetles would retract all their appendages. The histerids were not injured by the ants and ran away from them after a short struggle. The Euxenister immediately rubbed workers for a few seconds. However, shortly after leaving a worker, one histerid was again attacked. Three workers pulled legs on opposite sides, and the histerid appeared unable to pull away from them. Two other workers joined the attack and pulled on the dorsolateral thoracic carinae moving the histerid a few centimeters across the nest. Twice workers appeared to try to sting the Euxenister without success. The maximum number of workers which joined in the attack was seven; but when four of these released their hold, the histerid was able to drag three workers which were pulling on it toward an area with fewer workers. After a fight of seven minutes, the histerid pulled away from the ants and immediately got on the back of a large intermediate worker and again rubbed. The histerid did not appear to be injured in any way by the army ants. It is clear that the legs of this beetle are not as easily amputated as those of most insects which the army ants were seen attacking. The histerid kept its antennae hidden when the ants were attacking it. The two histerids placed in this nest were not attacked for at least several hours after the above encounters. Moreover, one large intermediate kept its mandibles spread open while a histerid stood between them and rubbed the ant's head. On the following day, several workers briefly pulled the histerid, but this encounter lasted only a few seconds. Later several workers appeared to be attempting to sting one histerid, and it retracted all its appendages in as far as possible. After several seconds, the histerid dashed away. Although the above observations do not give any clear indication that the rubbing by the histerid prevents or lessens attacks by the workers, these data show that in one case Euxenister was attacked primarily when it was first introduced into the laboratory nest. Moreover, these observations prove that even though it has trichomes, Euxenister caroli is subject to attacks by its host. Since both booty and some larval brood were in the laboratory nest and the workers had only been in the laboratory for four days, the workers were not induced by starvation to attack the beetle.

Euxenister caroli also spreads its mandibles wide and licks the surfaces of workers with its other mouthparts. However, most feeding by this species seems to be done by mouth-to-mouth trophallaxis with the workers. In one case a histerid and ant started such feeding in a fraction of a second, and it was not possible to determine whether any particular type of antennal or other contact was preliminary to the actual feeding. Both ant and histerid reared upward and each partially supported the other. The *Euxenister* sometimes had just its hind legs on the floor of the nest; the ant usually had its middle and hind legs on the floor. The dorsum of the histerid was approximately vertical. The mandibles of the worker were wide apart, and its other mouthparts were closely pressed against or interdigitated with the mouthparts of the histerid. The mouthparts were together for at least 45 seconds in the longest feeding observed. Even though such pairs frequently shifted their positions, they kept their mouthparts together. No fluid could be seen around the mouthparts, but presumably the histerid received something from the ant. Similar observations of such mouth contact between workers of *burchelli* and *Euxenister caroli* were made about five times.

In addition to the above observations which are assumed to be feeding, the *Euxenister caroli* also fed on larvae of *burchelli*. This histerid was seen to pierce the subapical abdominal segment of an active, uninjured larva. The larva reared up and pushed its head against the histerid when it was bitten. The beetle immediately drank some of the fluid oozing from the wound, and soon a staphylinid, *Vatesus panamensis* (Mann), a thysanuran, *Trichatelura manni* (Caudell), and a *burchelli* worker also fed at the wound. In laboratory nests the army ant workers usually eat the larvae from their own colonies but probably would not have attacked their larvae after four days with booty still available. Some cannibalism of cocoon broods by E. burchelli has been observed in the field, and it is possible that this was started by Histeridae or other guests.

In addition to mouth-to-mouth trophallaxis and feeding on larval brood, Euxenister caroli strigilated over or licked the surfaces of workers while riding on them or while standing next to them. This type of feeding was seen less frequently and is probably relatively unimportant for the nutrition of Euxenister.

On one occasion two staphylinids, Ecitomorpha nevermanni Reichensperger (1679), rode almost constantly for four hours on the backs of two histerids as the latter were rubbing workers. The staphylinids did not appear to interfere with the rubbing in any way. As the Euxenister caroli rubbed its legs against the lateral parts of its body, it repeatedly pushed the staphylinid's legs off of the dorsolateral carinae. The staphylinid constantly shifted its position and grasped other parts of the histerid's carinae. Probably the histerid was unable to reach the dorsal parts of its pronotum and elytra with its legs to remove the staphylinid. Ecitomorpha nevermanni also cleaned the surfaces of Euxenister caroli with its mouthparts in the same manner in which the staphylinid went over the workers.

About 24 hours after a male and female Euxenister caroli (1235, 1236) had been put in a laboratory nest, they copulated for five minutes. Before actual copulation (at 9:37 a.m.) the male rode on the back of the female for two to five minutes and also rode on her for a minute after copulation. Throughout the mating the beetles ran around in the laboratory nest. During copulation the female part of the time had her mouthparts touching the mouthparts of a worker in the type of trophallaxis described above. On the following evening (at 6:15 p.m.) the same two histerids were again seen mating. During this copulation the female climbed onto an intermediate worker and rubbed the ant's head and alinotum and her own body. Later the pair of histerids ran into the main cluster of workers where they could no longer be seen.

Euxenister wheeleri Mann: In emigration columns and bivouacs of *E. hamatum*: 13 March 1955, 29 February to 8 August 1956, colonies '55 H-E, E-121, E-123, E-141, E-159, E-162, E-221, E-243 (25♂, 20♀).

Euxenister wheeleri was described from one specimen taken with *hamatum* on Barro Colorado Island in 1924, and I know of no subsequent published records. The above records for *wheeleri* from eight colonies of *hamatum* suggest the hypothesis that the four known species of *Euxenister* are each restricted to a single species of host. In addition to *caroli* from *E. burchelli*, *asperatus* Reichensperger (1923b: 249-252) was found with *E. quadriglume*; and *breyeri* Bruch (1931: 392-395) was found with *Ectatomma quadridens* Fabricius. The latter host record is surprising; and since *breyeri* lacks the large lateral carinae on the pronotum and elytra considered important generic characters by Reichensperger, it may belong in another genus.

All major aspects of the behavior of *Euxenister wheeleri* and *caroli* appear to be identical. Where observations on *wheeleri* repeat some given above for *caroli*, they will be mentioned briefly in order to strengthen the earlier generalizations; but the emphasis will be placed on possible differences noted for *wheeleri*.

All specimens of *Euxenister wheeleri* which were seen during emigrations were in the middle period (like *caroli*) when most of the brood was carried. Although many worker cocoons may be carried on the first emigration of a nomadic phase of *burchelli*, nearly all the callow workers have emerged before a colony of *hamatum* starts a nomadic phase. Consequently, if most of the booty has been carried before *Euxenister* and the young brood appear in the column, this histerid is forced to run to the new bivouac. The best example of this was the first nomadic emigration of colony E-121 in which 16 *Euxenister wheeleri* were seen running between 7:15 and 8:45 p.m., and not a single individual was riding. This colony was watched continuously from 4:20 p.m., about one and one-half hours before the emigration started, until 9:40 p.m. when the emigration had ended except for a few stragglers milling around at the old bivouac. Probably every *Euxenister* in this colony was seen. Moreover, during an emigration on about the fourth nomadic day (colony E-141), all 14 specimens of *wheeleri* seen were also running. Another first nomadic emigration (colony E-168) contained seven *Euxenister*, but five of these rode on booty, one rode on the underside of the thorax of a large intermediate worker, and one ran. It appeared that more histerids rode on booty in this emigration because a greater amount of large larval booty was carried, but no quantitative samples of booty were made. It is strange that although both *caroli* and *wheeleri* frequently rode on major and large intermediate workers in laboratory nests, only one *wheeleri* was seen riding on a worker in an emigration. After the larval brood was half grown, an increasing proportion of the *Euxenister* rode on them. Sometimes the histerids were partially dragged as they hung on the side of a larva, and sometimes the histerid appeared to kick or "run" with one or two legs while the others held onto the larva.

Euxenister wheeleri was never seen in raid columns or outside the bivouac during the day. The general appearance of the two species of Euxenister is the same, and both have dense hairs on the inner surfaces of all tibiae and the large dorsolateral carinae on the pronotum and elytra. Eu. wheeleri rides both on the underside of the worker's gaster and on the alinotum. However, the histerid only rubs the alitrunk with its legs when it is on top of it, possibly because the rubbing elsewhere would interfere with the ant's running. The histerid rubs the gaster when the beetle is either on top or under it and whether or not the ant is running. No worker was seen to pick up this histerid, but wheeleri sometimes climbed onto the underside of a head of an ant and rode there. Laboratory observations indicate that wheeleri concentrated its rubbing to a greater extent on the heads of major workers than did caroli. Since the major workers of hamatum have shiny, oily-appearing heads, whereas the heads of burchelli majors are dull, perhaps the histerid can rub more material off the heads of hamatum majors. However, wheeleri did not confine its rubbing to these heads; and since measurements of the exact duration of rubbing on all parts of the ants were not made, the proportion of rubbing on the heads of either host can not be estimated. When four to 14 major workers were put in a dish with one wheeleri, the histerid usually ran over several or most of the majors before rubbing the head of one of them. In all cases the histerid ran directly to the major's head. The only times a Euxenister appeared to irritate the ants were when it hung on the antennae of major workers or when the histerid was active around the maxillae of a major. Majors repeatedly struck histerids with their front or middle legs when the beetles were moving around the ant's maxillae. The histerids' rubbing of the ant's mandibles and head was ignored. One time a histerid appeared to be holding onto a major worker's maxillae or the membrane next to them by only its mouthparts. The histerid's body was oriented transversely under the ant's head with the left front and middle legs sometimes hooked on the ant's labrum. The major reared up, gave three large jerks, and repeatedly scratched at the histerid. Two intermediate workers ran up to the major and scratched at the histerid with their legs but did not pull it off the major. When the workers scratched at the histerid with their legs, the histerid kept its legs pressed against its own body. One of the intermediates and the major bent their abdomens around in the stinging position, but no sting could be seen. Probably the workers are not able to sting *Euxenister*. Twice the labium and palpi of the major were pushed against the ventral side of the histerid's thorax and abdomen, but these mouthparts did not move the histerid.

Although *wheeleri* was not seen to rub the area between the dorsolateral carinae with its legs, when climbing on the mandibles and legs of a major worker, the histerid rubbed its entire dorsum against the ant's mandibles, head and thorax.

The only time *Euxenister wheeleri* was attached by the ants in a laboratory nest was when a specimen was isolated from its host for two days. This histerid retracted its antennae, but its legs were pulled almost straight by several workers which prevented its escape. Within ten minutes the attack became less intense, and the histerid ran to another part of the nest where it avoided further attack for at least a half hour. During the attack the ants appeared to lick and chew on all surfaces of the histerid including the mouthparts; but although no damage was done to the heavily sclerotized beetle, weaker insects undoubtedly would have been killed. At the end of 26 days one *Euxenister wheeleri* was alive and active, but nearly all the workers taken from the host colony at the same time were dead or dying. Other myrmecophiles, such as the staphylinid *Vatesus* and the thysanuran *Trichatelura*, were killed more readily than was *Euxenister* by *hamatum*.

Euxenister wheeleri was seen to feed (?) by mouth-to-mouth contact with workers of all sizes, but rarely licked the surfaces of any ant. *Chrysetaerius iheringi* Reichensperger was reported to be fed and licked by *E. quadriglume*, and the histerid was supposed to enter into "oral and antennal communication" with its host (based on observations by Zikan and the unnamed Rev. Franciscan Fathers of St. Anthony College, Rio Negro published by Reichensperger, 1924a: 132; Seyfried, 1928: 56-57). No details on this behavior were given, and I know of no other accounts of similar behavior for other histerids found with army ants. In addition to its presumed feeding from the mouths of the host, *Euxenister wheeleri* also fed on booty and young larval brood and drank water from paper. It did not feed on dead workers of *hamatum*.

As mentioned above both species of *Euxenister* are much more frequently found on major workers than on queens or smaller workers. Although there was no evidence that the intermediate or minor workers were attracted to the major workers or licked them more than other workers, all army ant workers were usually strongly attracted to their queens which they licked frequently in laboratory nests. When no major workers were in a dish, *Euxenister wheeleri* rubbed the thorax and head of a queen (E-123) and rode on the underside of her thorax. The histerid also licked the alinotum of the queen for a few seconds. However, when one major worker was added to the dish, the *wheeleri* immediately abandoned the queen and rubbed and rode on the major almost constantly.

Latronister rugosus Reichensperger: In emigration columns and bivouacs of *E. vagans*, 30 April to 26 July 1956, colonies E-154, E-180, E-219 (1685, 1888, 1889, 2167, 2199) (4♂, 1♀, 1 sex?).

Latronister rugosus was described from one specimen taken at Hamburg Farm, Costa Rica, with *E. hamatum*. Two additional specimens were found at the same locality attached to petioles of *hamatum* workers running in columns (Reichensperger, 1932: 8-10; 1939b: 300). The fact that the three Costa Rican specimens were found with *hamatum* and the Panamanian specimens were found with *vagans* places some doubt on the determination of the latter specimens. However, three of the specimens taken on Barro Colorado Island were also seen attached to the petioles of workers. One specimen (1888) appeared to have its legs around the petiole of a large intermediate worker. The worker was not carrying anything, and it was not determined whether this histerid was holding onto the petiole with its mandibles. In a laboratory nest five histerids (1888, 1889, 2167 and 2199) were repeatedly seen riding and climbing on large worker ants (see figures 57 to 60) but never on major or small intermediate workers. While the beetles climbed on the ants and frequently bit their legs or antennae (see figure 60), the workers always stood quietly. Probably the histerids clean material off the surfaces of the workers, but I could not determine whether *L. rugosus* was licking or strigilating as it bit the ants. The histerids did no visible damage to them, and the workers never attacked the histerids. Several times as a histerid tried to climb on a gaster of a worker, the ant removed the histerid with its mandibles but did not hold or injure it. In the normal position, judging from the laboratory observations, the histerid grasped the abdomen with the mandibles between the two petiolar segments. The histerid rode ventrally with its front legs folded tightly against its body, and the middle and hind legs sometimes touched the worker. Although in attaching to the worker, the rugosus climbed on the posterior end of the abdomen, once its mandibles got a grasp on the petiole the legs did not cling to the ant. The middle and hind legs kicked for two to four seconds alternating with a quiet period of about one second. This intermittent kicking had no obvious function. During this kicking the sides of the femora and tibiae did not contact the ant, but the tarsi sometimes did touch the gaster.

Both a male and female of L. rugosus at one time climbed on the gaster of a callow worker. The beetles were not mating, and the worker turned its gaster under its body and removed the histerid riding on the posterior end. The histerid at the anterior end of the gaster was not disturbed by the ant.

Mesynodites confirmatus Reichensperger: In an emigration column and refuse deposits of E. burchelli (2♀, 8 sex?).

The genus Mesynodites includes about 45 species known from army ants and several other species known primarily from Atta. Mesynodites spp. may stay at the nest after the army ants have emigrated, and Bruch (1926: 18) found over 300 M. ciliatus at one bivouac site. Most of the species of Mesynodites appear to be found in the refuse deposits or in the dirt around the periphery of the bivouacs. This generalization holds for M. confirmatus except for the specimen (1368) seen apparently being carried between the mandibles of a worker in an emigration column. It is possible that the beetle had climbed up on the worker and was simply riding underneath the ant's head. When it was put in a laboratory nest with workers from the host colony, *M. confirmatus* ran around primarily at the edge and avoided the ants. In the nest it was not killed during two days but never was seen to ride on or be carried by any ant. One specimen of *confirmatus* was also found in a column in Costa Rica, but it was not stated whether it was running, riding or being carried (Reichensperger, 1935: 190, 194-196).

Mesynodites obscurus Reichensperger: In an emigration column of *L. praedator*, 30 May 1956, colony E-177 (1876) (1 sex?).

One specimen of *Mesynodites obscurus* was aspirated with workers from an emigration column of *L. praedator*; the histerid probably was riding on or being carried by a worker. This same species has been found with *L. coecus* and *praedator* in Costa Rica and Brasil (Reichensperger, 1939a: 119-122).

Mesynodites ?*bifurcatus Mann*: In bivouac sample of *E. hamatum*, 26 July 1956, colony E-221 (2194) (1♀).

Mesynodites bifurcatus Mann was described from one specimen found in a cluster of *E. hamatum* on Barro Colorado Island (Mann, 1925: 170-171). We found one specimen in masses of larvae and workers taken from the ground after a bivouac of *hamatum* had been knocked down during an emigration.

Mesynodites n. sp.: In one raid column of *Nomamyrmex esenbecki*: 12 February 1956, colony E-102 (1148) (1♂, 1♀).

One male and one female of a new species of Mesynodites were found running in the middle of a raid column of Nomamyrmex esenbecki at 9:45 a.m. No additional specimens were seen in the columns of this colony which were watched for several hours, nor were any found in raid and emigration columns of a number of other colonies of the same host.

Nymphister n. sp.: In an emigration column of E. hamatum, 18 March 1956, colony E-121 (1535) (1 sex?).

Nymphister simplicissimus Reichensperger (1933a: 188-190), described from a specimen taken with E. burchelli in Costa Rica, is the only described species in the genus. The new species was following the chemical trail of E. hamatum at 9:30 p.m. after all the ants had left the old bivouac. I watched the beetle as it followed the emigration route for the first two meters from the site of the old bivouac.

Paratropinus scalptus Reichensperger: In refuse deposits of E. burchelli, three colonies (2♂, 2 sex?).

This species appears to be primarily found in refuse deposits, but Reichensperger (1935: 199-200) reported it in a column of E. burchelli in Costa Rica.

Psalidister burchelli costaricensis Reichensperger: In a refuse deposit and emigration of E. burchelli, 20 Febrary 1956 and 7 March 1956, colonies E-111 and E-110 (1209-I, 1399) (2♂).

Reichensperger (1926: 197) reported that this species feeds on weak workers and ant larvae. This conclusion was apparently based on his finding parts of ants or larvae in the mandibles of preserved histerids. However, such evidence is not reliable since the histerids will bite at any object when they are placed alive in alcohol. Moreover, if a living histerid with something between its mandibles is placed in alcohol, the beetle may open and shut its mandibles; and the object most likely will be released.

Psalidister n. sp. 1: In refuse deposits and one bivouac of *E. burchelli* (2♂, 4♀).

This species is primarily a refuse deposit species. One specimen was taken in a bivouac sample (1040), but this sample included considerable amounts of detritus from around the edges of the bivouac.

Pulvinister nevermanni Reichensperger: In emigration columns and bivouacs of *E. hamatum*, 2 March to 8 August 1956, colonies E-121, E-123, E-127, E-141, E-211, E-243 (9♂, 7♀, 4 sex?); same locality and host, taken from bivouac in middle of statary phase, 23 March 1948 (T. C. Schneirla) (1 sex?).

Reichensperger (1933b: 300) wrote that one could expect to find this species carried by the workers since the prothorax and legs offer convenient handles. The first time I saw *P. nevermanni* under the head of a major worker, I thought that the ant was carrying the histerid. However, laboratory observations showed that the major workers never pick up this histerid. *Pulvinister nevermanni* climbed onto the major workers and always rode under their heads. The histerids usually held onto the workers' heads with their legs, but sometimes they may have used only their mouthparts. *P. nevermanni* was seen riding in this position 14 times along emigration columns of *hamatum*. In addition, three beetles (1520, 1521 and 1522) were seen riding in the same position repeatedly in a laboratory nest. Not only did this histerid never ride in any other position, but it never rode on workers smaller than the majors. Two additional specimens were seen running in an emigration column.

Our records from six colonies of *E. hamatum* together with the type series from Costa Rica suggest that *P. nevermanni* is restricted to this host. Since 14 out of 16 specimens taken from emigration columns were found on major workers, one might expect to find this histerid whenever the majors are in the columns. Our limited observations indicate that this may not be true. The beetle was never seen along raid columns; and during the only two emigrations when at least five specimens of *nevermanni* were taken, it was slightly more abundant near the ends of the emigrations. Some specimens were seen while the brood was being carried, but about half of the *Pulvinister* were seen after the brood. During the same two emigrations, *Euxenister wheeleri* was seen primarily before *Pulvinister nevermanni*, and *Euxenister* was not seen after the brood had passed.

Symphilister hamati Reichensperger: In emigration columns and in a bivouac of *E. burchelli*, 5 March to 20 May 1956, colonies E-110, E-148 (2♂, 4♀).

The type of *Symphilister hamati* was found with *E. hamatum* in Costa Rica, and *collegianus* Reichensperger, the other species in the genus, was found with *E. burchelli* in Brasil and Costa Rica (Reichensperger, 1923a: 323-325; Borgmeier, 1948b: 391-392). The variation among the specimens reported in the latter paper and the conflicting host records cast doubt upon the determinations of all *Symphilister*.

All specimens of S. hamati observed by Zikan were being carried by the ants in their mandibles (Reichensperger, 1926: 199-200; 1929: 259-261). However, the beetles were described as hanging pendant between the front legs of the ant, and no ant was seen to pick up a beetle. It is quite likely that the histerids were actually riding, because I never saw Symphilister hamati being carried but three times saw it riding under thoraces of workers. The beetles were close enough to the heads that one could easily conclude that the histerids were being carried. Five specimens of Symphilister hamati were taken from one emigration column during the period when brood was being carried, and no other specimens of this histerid were taken from other emigrations.

Troglosternus ecitonis Mann: In a refuse deposit of E. hamatum, 23 June 1956, colony E-191 (2♂, 1♀).

Barro Colorado Island is the type locality for Troglosternus ecitonis which was described from five specimens taken with a cluster of E. hamatum (Mann, 1925: 166, 172). During our collecting at the same locality we found three additional specimens at 10:30 p.m. in refuse on the ground directly under the former position of a bivouac of hamatum after all except about 50 ants had emigrated. Two of the histerids were copulating as they walked around in the refuse, and they were still (or again) in copulo from 8:00 to 9:00 a.m. on the following morning. The three histerids were put in a laboratory nest with Vatesus, Trichatelura and workers from the host colony; but the histerids avoided the ants and other guests and readily retracted all their appendages whenever an insect touched them. It is unlikely that the ants could carry such smooth and round beetles. Since the three specimens had not joined the emigration up to 10:30 p.m., it is possible that this species flies from one bivouac to another. However, *Troglosternus lisae-vedouae* Reichensperger has been reported from columns of *L. coecus* (Reichensperger, 1938: 78-80).

New genus and new species 4: In emigration and backtracking columns of *E. vagans*: 26 July and 7 August 1956, colonies E-219, E-240 (1♂, 1♀).

One specimen probably was riding on a young alate male in the emigration of colony E-240. This histerid also held onto the coxae of a male by its legs and rode facing anteriorly under the male as the ant walked around in a laboratory nest. I could not see whether the histerid also used its mandibles to hold onto the male army ant, but it did not use its mandibles later when it rode on the male's alinotum. Twice in a laboratory nest this histerid was seen riding on the undersides of heads of intermediate workers. The mouthparts of the histerids were directly under the mouthparts of the ants. These workers clearly were not holding any parts of the histerids in their mandibles. In both cases the ants appeared to run more quickly than those without histerids.

Other new genera and species: Three additional new genera and species were taken from bivouacs or emigration columns of *E. vagans*, *dulcius crassinode* and *Nomamyrmex esenbecki*. Each species is represented by two or four specimens found in preserved samples of ants.

Hymenoptera

The only myrmecophilous Hymenoptera found with army ants are small parasitic wasps most of which belong to the family Diapriidae. Ferrière (1929) and Borgmeier (1939) have reviewed about 23 species of diapriids described from specimens found with army ants. Most of these species look somewhat like ants, and some appear to mimic the ants closely in form and color. Some of these diapriids never have wings, and other species lose their wings after getting into an ant colony. Tufts of hairs on the head, thorax and abdomen have been described and are considered to be trichomes (Ferrière, 1929: 165; Borgmeier, 1939: 545). Some species have been taken as the wasps were running in columns of army ants, and Mann (1948: 100) reported seeing a wasp [probably a diapriid] "stop running for a moment, whereupon one of the ants picked it up, held it underneath its abdomen in the same manner that it would carry one of its own young, and resumed the march." Diapriids have been found with the four main genera of Ecitonini, and several species are known from two species of host. The above three authors have speculated that these wasps are parasitic on the army ants or their guests; but as far as I am aware, there has been no further information published on the biology or behavior of these diapriids.

No living diapriids were seen during this study, but six specimens were taken when workers were preserved in the field. These specimens have not yet been determined.

IV. SUMMARY AND CONCLUSIONS

THE BEHAVIOR OF ARMY ANTS

Probably the most important conclusion from this study is that nearly all the additional observations on the behavior of army ants support the conclusions indicated by Schneirla (1933, *et seq.*). However, his work was initially concentrated on *Eciton hamatum* and *burchelli*, probably the most atypical species of Ecitonini because they are the only ones with epigaeic bivouacs. My observations, although much more limited than those of Schneirla, include a wider range of species and some aspects of the behavior of the ants not mentioned by him. These observations indicate a somewhat greater diversity in behavior within the army ants and especially within the genus *Eciton s. str.* than has been reported so far. Consequently, the behavior attributed to *Eciton* by Schneirla and other authors may not apply to the majority of species within the genus.

Raids: Most species of army ants obtain food by means of column raids with small groups of ants entering new territory at the ends of columns advancing from the bivouac. *E. burchelli* and *Labidus praedator* have, instead, swarm raids, *i.e.*, large masses of ants advancing at the fronts of fan-shaped areas of anastomosing columns. The base column of *praedator* is usually subterranean near the bivouac and as the swarm front advances, the subterranean columns are extended while the epigaeic ones disappear. In contrast, the basal columns of *burchelli* are always epigaeic all the way back to the bivouac. Compared with the raids of *burchelli*, the raids of *praedator* are usually much smaller, shorter in duration, more frequently nocturnal, and more often meander and double back over the area just raided. Although raids of *burchelli* may begin at dawn and occasionally last until somewhat past sunset, they never start during the night like those of *praedator* which can be found at any hour. L. coecus, which appears to be closely related to praedator morphologically, has epigaeic raids almost exclusively at night with a raid pattern intermediate between swarm and column types.

Although no detailed study of the prey has been made, numerous observations indicate that species of army ants when raiding in the same places may attack different species of booty. All species of army ants studied captured more ants than any other kind of prey but never captured any species of Ecitonini. The size of the prey species is somewhat correlated with the size of the army ant attacking it. However, there are cases where two species of army ants having workers of equivalent size differ in their attacks on potential prey. For example, burchelli readily and commonly attacks Paraponera clavata which appears to be avoided by hamatum. All species apparently kill more arthropods than they eat, and some species or groups of arthropods are probably never attacked or killed. None kill vertebrates frequently, as do certain Old World Dorylinae.

Bivouacs: All species of army ants probably have only temporary nests, called bivouacs, unlike the more or less fixed nests of most ants. The frequency or regularity of emigrations is unknown for most species. Epigaeic bivouacs are typical for only E. hamatum and burchelli, but the ability and habit of forming hanging clusters was found among other species of Eciton and Neivamyrmex even though their subterranean bivouacs do not consist primarily of such clusters. The legs of Ecitonini are relatively long and thick compared with those of most other ants, and these characteristics of the legs may be important adaptations for the clustering behavior. I do not believe the opposed recurved tarsal claws were developed with the evolution of such clustering because similar claws are present on many species of nondoryline ants including Ponerinae.

The epigaeic species of Eciton will occasionally make a symmetrical bivouac in the form of a cylinder or truncated cone on the inside or underside of a log. However, most epigaeic bivouacs are much more complex in shape because they hang upon irregular cavities or brush heaps. Subterranean bivouacs seem to have an even more complex shape and are usually subdivided into many small clusters because the ants use existing cavities with slight modifications and do not dig an entire nest or bivouac site. In contrast to the epigaeic species which keep their brood in the center of their relatively homogeneous bivouac, the brood in the subterranean bivouac may be found in any position. In addition, the species of Neivamyrmex in the United States apparently move their larvae, prepupae and pupae up to the underside of warm rocks during the day and shift the brood back into the soil when the rocks cool.

Refuse Deposits: All army ants presumably put dead ants and the remains of booty in refuse deposits a short distance from the bivouac. The refuse deposits of epigaeic species are the only ones which can be easily studied. There is little refuse outside colonies of hamatum because this species captures primarily softbodied insects. However, the refuse deposits of burchelli are extensive, containing thousands of living arthropods and sclerotized remains of arthropods. Most of the material in the refuse deposits is carried there by the workers, although some is dropped directly from the bivouacs. Most of the refuse is eaten or carried off by scavengers within a few days.

Emigrations and the Nomadic-Statary Activity Cycle: The emigration columns of Labidus, Nomamyrmex and Cheliomyrmex sometimes are bordered by dirt walls or are completely covered by arches made of loose dirt by the workers. These walls or tunnels never were seen along the entire route but seemed to be constructed primarily where the ants left underground passages and moved on the surface of the ground. Exposure to light including direct sunlight did not stimulate the ants to build or extend these tunnels. *Labidus* and *Nomamyrmex* have been considered closely related on the basis of morphology, and this relationship is supported by the above behavior. *Eciton* and *Neivamyrmex* do not make walls of dirt along their columns.

Several additional cases are reported in which one species of army ant has followed for many meters a chemical trail made by another species of army ant. However, little is known about the chemical nature of these trails and how they may affect the direction of raiding and emigration.

Scattered observations on various species support Schneirla's hypothesis that the "condition" of the brood (primarily its age or properties dependent upon its age) is the most important factor influencing the start and duration of the nomadic phase (nest site or bivouac moved more or less daily for two to three weeks) and the statary phase (bivouac at one site for about three weeks). Although most species of army ants appear to have synchronous broods necessary for a precise nomadic-statary activity cycle, even with such broods the cycle may not be as regular as that described by Schneirla for *hamatum*. A nomadic phase with several nights without emigrations is typical of *Neivamyrmex opacithorax* and *nigrescens* which have synchronous broods. It is clear that *Labidus* sometimes has broods which are nonsynchronous, and the relatively large number of physogastric queens of *Labidus* which have been found suggests that their oviposition period may be longer than that of *Eciton*. It has been reported several times that bivouacs of *Labidus* remained in the same spot for several months or longer, but no information is available on the type of brood present in these bivouacs.

Although I agree with Schneirla's main theory that the brood or broods are the primary stimulus inducing raiding and emigrating, I believe he has gone too far in discounting the influence of the amount of booty on the activity of the ants. The amount of booty in an area affects the direction, distance and duration of raids and emigrations. Although it has not been demonstrated, it would appear that the amount of food within bivouacs must influence the amount of activity of the larvae, and thus, their stimulation of the adults. As the larvae get larger, one might expect that since they presumably stimulate the adults more and also require more food, the distance that the ants raid and emigrate would increase. The total distance of raiding appears to increase, but most of this increase appears to result from raiding in several directions rather than in one direction from the bivouac. The emigration distances of *E. hamatum* and *Neiv. nigrescens* do not increase throughout the nomadic phase and may be greatest in the center of the phase.

Division of Labor and Integration: Some species of Ecitonini are exceedingly polymorphic, and the workers within a species often vary greatly in size and morphology. The following observations summarize rather incidental observations on the different castes and on workers of various sizes. The major workers of *Eciton* take part in the formation of hanging clusters and assist in capturing booty and attacking predators or any animal which disturbs a colony. A disturbance of a column of army ants or part of a bivouac often results in an increase in the number of majors at that point. Large workers of *Labidus coecus* were attracted apparently in a similar manner to the site of a struggle when smaller workers had difficulty transporting peanuts. These large workers assisted in dragging the peanut toward the bivouac. However, the largest workers of coecus, like those of L. praedator, probably do not leave the bivouac on raids. Compared with the largest workers of other genera of Ecitonini, the major workers or soldiers of Eciton both morphologically and behaviorally come closest to forming a distinct caste. The majors of Eciton were never seen to carry any booty or brood, not even the huge larvae of reproductives for which the large sickle-shaped mandibles of the majors might seem well suited. During emigrations the major workers are most abundant near the queen and make up a high percentage of the workers in the retinue accompanying her. When a bivouac of Eciton is torn apart, the queen is usually surrounded by a large number of excited majors. However, in an undisturbed bivouac the smallest workers usually form a tight ball around the queen.

Major workers were never seen being carried by any other workers, and the frequency with which workers are carried varies inversely with their size and age. Callow workers apparently do not take part in raids until at least a day and probably not until several days after they emerge. However, on the first nomadic emigration of burchelli a few callow workers carry cocoons or dark workers. The number of workers which are carried on an emigration increases toward the end of the emigration. Numerous workers which were being carried were collected, and all ran around actively and showed no sign of injury. When carrying adults or brood, workers typically placed their mandibles around the alinota of adult workers, around the thoracic segments of larvae and around the posterior ends of cocoons. It was discovered that worker larvae of Nomamyrmex, like those of *Eciton* and *Labidus* spin cocoons. Worker larvae of *Neivamyrmex* do not spin cocoons. Queens of *Eciton*, *Neivamyrmex* and *Nomamyrmex* were all observed running in emigration columns, and even physogastric queens of the first two genera were observed running. Workers running in the retinue of a queen were never seen to carry or pull the queen and probably hindered her movement much more than they helped her. The retinue increases the extent of an ant roadway in areas where the queen might have more difficulty running than the workers, and probably the retinue would protect the queen from a potential predator. The queen most commonly emigrates after three fourths of the colony has left the old bivouac but may emigrate after one third to one half of the workers have left. (Additional conclusions on the timing during emigrations are given below in the section entitled When Myrmecophiles Emigrate.)

Workers appear to be attracted more to the gaster of their queens than to any other part of her body. The workers rarely were attracted to the anal region or mouthparts. Workers were never seen to feed queens of *Eciton*, *Nomamyrmex* or *Neivamyrmex*. Observations on single queens of these three genera suggest that the relative attraction of workers to the segments of a queen's gaster may be quite different depending upon the genus or species concerned as well as upon the individual.

The mating of one old *Eciton* queen in the laboratory supports the hypothesis that army ant queens mate more than once and may mate each year when sexual broods are produced. Most male army ants probably live a few days and seldom live more than three weeks. It is likely that the males are photonegative and unable to fly for one to three days following their emergence and may become photopositive only after flight.

Relations with the Physical Environment: Schneirla's hypothesis that males of E. *hamatum* and *burchelli* are produced in the dry season or dry periods is supported by additional records. However, the direct or indirect effect of the dry season apparently does not act simultaneously or in the same manner on these two epigaeic species because males of *burchelli* are produced somewhat earlier than those of *hamatum*. Moreover, it is clear that queens of Ecitonini including some species of *Eciton* must lay eggs during the rainy season which develop into reproductives. Some other factor such as possibly the onset of the rainy season or changes in day length must play a part in the production of the sexual broods.

Except for changes in behavior when broods of reproductives are in colonies, there do not appear to be any distinct differences in raiding or emigrating between rainy and dry season conditions for the epigaeic species of *Eciton*. The subterranean species of army ants more frequently have diurnal raids and emigrations on the surface of the ground on cloudy, humid or rainy days than on sunny dry days. Thus, these species are more commonly seen during the rainy season than during the dry season. One exception seems to be *Neivamyrmex postcarinatus* Borgmeier, a species known only from Barro Colorado Island where it was found five times during the dry season but was not seen during the rainy season. The hypotheses of Schneirla concerning the effects of light, temperature and humidity on the beginnings of raiding, the siesta period and emigrations are all considered overly simplified, and he has not supported them by data on these environmental factors.

Arthropods Associated with Army Ants

Diptera Associated with the Swarm Raids

There are three important genera of flies found over and near swarm raids of army ants in Panamá. These three genera are Stylogaster (Conopidae), and Calodexia and Androeuryops (Tachinidae). All three genera are mainly found over the areas where the raiding ants are concentrated at the front of swarms and up to two meters in advance of the swarm fronts. There is no good evidence that any flies are found frequently in the fan area behind the swarm front or over raid or emigration columns. When the flies from the swarm front are found in the fan area, it is usually because a specific host insect has remained there or has fled to the fan area. These flies are found neither within the nests nor running in the ant columns. Their association with the ants seems to be to take advantage of host insects flushed from the litter by the ants. Of course only those that escape the ants are of importance to the flies.

Stylogaster differs in its behavior from the other two genera by its almost constant hovering. Calodexia and Androeuryops usually rest on low objects and frequently shift position to avoid the ants. No species of Stylogaster has been reared, but it appears that those species found over army ant swarms are parasitic on cockroaches. This is indicated by their darting after cockroaches driven out by the ants and by the finding of at least one egg on a cockroach. However, their eggs have been found also on Calodexia and Androeuryops which may possibly be hosts for the conopids. A first instar larva of Stylogaster is described from an egg found on a Calodexia.

Calodexia males are extremely rare near the ants, but the females are very common, over a thousand accompanying a large swarm raid. Large numbers of *Calodexia* are attracted to swarms of both *Labidus praedator* and *Eciton burchelli* at any time during daylight and twilight. These flies appear in the first ten minutes after the start of a raid, and increase to about 50 flies within a half hour. They probably locate the swarm front by the odor of the ants. Of 12 species of *Calodexia* compared, six show a significant preference for raids of one or the other of the swarm-raiding ants, *i.e.*, *L. praedator* or *E. burchelli*. The greater abundance of these species over one or the other species of ant is probably attributable to differences in the raiding behavior. The dissimilarity in raiding results in qualitative and quantitative differences in the arthropods driven out by the ants.

Calodexia is larviparous and probably deposits larvae on the surface of a host instead of inserting them. Brief descriptions of the three larval instars are given. Larvae of *Calodexia* were found in crickets (Gryllidae) and cockroaches (Blattoidea), and a few adults were reared from these hosts which are the most common large Orthoptera found in the litter of the forest floor.

Males of *Androeuryops ecitonis* are almost twice as abundant as females over the swarm raids of army ants. The behavior of *A. ecitonis* around the swarms appears to be similar to that of *Calodexia*, but no host is known for the species. It is oviparous and its ovipositor indicates that the eggs are laid inside the host. Unlike *Stylogaster* and and *Calodexia*, the numbers of *Androeuryops* were much higher in the dry season and early rainy season than they were later in the rainy season.

All three genera are thought to find their hosts by seeing them as they run or fly to escape the ants. Apparently these flies would be unable to find hosts without the aid of the ants or at least would be much less successful at finding hosts. The combined attack by the ants and these Diptera must kill a large number of orthopterans. Possibly less than ten per cent of the potential hosts within the area swept by a swarm raid escape death by either the ants or these flies; indeed, meager data indicate that 50 to 90% of the cockroaches and crickets that escape the ants are parasitized by *Calodexia* alone.

Although this study was done in Panamá, identical or related species of flies appear to be present throughout the range of the two ants with which they are associated. These ants, *Labidus praedator* and *Eciton burchelli*, range from southern México to southern Brasil in areas of wet tropical forest.

A revised key to the species of *Calodexia* and partial redescriptions are included.

In addition to the three most abundant genera discussed above, six other genera of flies were found over swarm raids of these ants and rarely or never at any other location. This circumstantial evidence suggests that their life cycles may be connected with the biology of the ants. These flies are a calliphorid, *Phaenicia purpurescens*, sarcophagids including four species of *Dexosarcophaga*, five species of *Nephochaetopteryx*, eight species of *Notochaeta*, and six species of *Oxysarcodexia*, and the muscid *Polietina ecitonovora*. Two of the species of *Dexosarcophaga* were reared from refuse deposits of *burchelli*, and it is probable that larvae were deposited directly in the refuse deposits. One species of *Notochaeta* was reared from a frog parasitized at a swarm raid which suggests that this fly may have habits analogous to those of *Calodexia* but larviposits on frogs escaping from the swarm raids.

Stylogaster is one of several genera of arthropods found associated with both the Neotropical and African Dorylinae. This genus apparently hovers over swarm raids of *Dorylus* (*Anomma*), but no detailed observations have been made in Africa. A common group of calliphorid flies in Africa and southern Asia snatches booty away from the driver ants, but similar behavior is not known for any flies found with Ecitonini.

Arthropods Found in Refuse Deposits of Army Ants

Arthropods were collected primarily from refuse deposits of *E. burchelli* because no other species of army ant has either large or readily accessible refuse deposits. Although a single newly established refuse deposit may contain several thousand arthropods, most of the adults leave within a few hours after the ants emigrate. The vast majority of arthropods found in the refuse deposits of *burchelli* apparently are attracted to these areas because of abundant food there. Many of the species, including most of the mites and nondoryline ants, probably are in the forest floor litter and merely become more concentrated in those areas where the booty refuse is deposited.

Other species of arthropods do not follow the emigrations of the ants but fly through the forest until they find refuse deposits, where these species probably breed. Some species probably are restricted to this habitat and fly from one bivouac to another. Among the species which have these habits and clearly do not follow the emigrations of the ants, the following have been reared from material collected from refuse deposits: two species of *Euryomma* and one species of *Neivamyia* (Muscidae), two species of *Dexosarcophaga* (Sarcophagidae), and some undetermined microlepidoptera. Numerous larvae of Staphylinidae and other beetles were found in the refuse, but a few attempts to rear adults were not successful. The staphylinid *Ecitopora* and some Histeridae such as *Omalodes*, *Mesynodites* and *Phelister* apparently fly from one bivouac to another; but some species in the latter two genera may also run in the emigration columns. A large number of wasps which are presumed to be parasites of Diptera must fly to the refuse deposits.

Another group of species emigrates along with the army ants or at the end of the column shortly after all the ants have left the bivouac site. Included in this group are the staphylinids *Tetradonia* and *Ecitophya*, some species of histerids in the genera *Mesynodites*, *Cheilister*, *Psalidister* and *Troglosternus*, and at least eight species of phorids. A few mites and Collembola probably breed primarily in the refuse deposits and emigrate by riding on the ants.

Myrmecophiles Found in Bivouacs and Columns of Army Ants

When Myrmecophiles are Found During Emigrations: In spite of the large amount of variation found among emigrations of army ants, there is an approximate sequence for the ant traffic and each species of myrmecophile. Better records for emigrations of all hosts will probably show that many myrmecophiles are restricted to or are most frequently found in certain parts of an emigration. This summary will emphasize generalizations which probably apply to emigrations of all army ants.

The first sign of an emigration may be an outpouring of workers along a raid route; however, it is difficult to judge when increases in traffic indicate an increase in raiding and when they indicate the start of an emigration. The start of an emigration may be more accurately defined as the time when the workers returning to the bivouac with booty turn around and carry the booty out along the same column. A large amount of traffic going away from the bivouac may physically push the booty carriers around but must not be the only factor in the reversal of these ants.

During this early transition period from a raid to an emigration column Phoridae and Staphylinidae can be found running in the column or more frequently along the edges of the column. These staphylinids are species which are scavengers on dead workers and on booty refuse or which are predators on living workers. Most of the staphylinids do not attack workers along the column but emigrate to the next bivouac. The phorids are primarily those species found around the edge of bivouacs in refuse deposits.

If a colony has a brood of callow workers or newly emerged males, these young adults are seen next in the emigration column. When males were present, laelaptid and neoparasitid mites, and limulodid and histerid beetles were found riding on them. There is no indication that the callow workers differ from old workers in the number of myrmecophilous (including parasitic) mites and insects on them.

The next major stage in an emigration is the period when the brood of eggs or larvae are carried. Shortly before the brood appears, myrmecophiles increase in number and reach their peak during the time when the brood is transported. Included in this group are *Calymmodesmus* and *Rettenmeyeria* (Diplopoda), *Trichatelura* (Thysanura), *Euxenister* (Histeridae), *Cephaloplectus* and *Limulodes* (Limulodidae), and *Vatesus panamensis* and *V. rettenmeyeri* (Staphylinidae). The Limulodidae appear to be the earliest to emigrate in the above group, and both the large *Cephaloplectus* and the minute *Limulodes* may be found running before the brood is carried. Because the millipeds run more slowly than the ants, the farther from the old bivouac that one watches an emigration column the later the diplopods will be seen until some of them run behind the end of the ant column.

The queen may emigrate when about one third of the colony has left the old bivouac, but usually she emigrates after three fourths or nine tenths of the workers have left. She most frequently appears shortly before or just after the last of the brood. Limulodidae (primarily *Cephaloplectus*) and occasionally circocyllibanid mites are the only myrmecophiles known to ride on queens in emigrations. It is possible that limulodids are more abundant running near the queen than in other parts of the emigration. Because major workers are much more abundant near the queen in emigrations, those myrmecophiles which are found almost exclusively on majors can be collected at that time. Included in this group are some species of Circocyllibanidae, Neoparasitidae and Macrochelidae and the histerid *Pulvinister nevermanni*.

Following the brood and queen the column usually decreases in width, and more adult workers are carried. After the emigration column decreases to less than half its maximum width, it probably will rapidly end. The ants in the last one to three meters of the column are much more hesitant in their running than the previous workers. These last ants stop frequently and run back toward the old bivouac for a few centimeters and then continue along the emigration route. Some of the workers may repeatedly run away from the emigration route for distances of about five centimeters and then rejoin the column. Some data suggest that the ants at the end of the column act as a "clean up squad" picking up workers and myrmecophiles lagging behind. At this time *Neivamyrmex opacithorax* workers were even seen to pick up pieces of dirt and sticks and carry them short distances toward the new bivouac.

Close to the end of the ant column and after the last ants, there is a marked increase in those myrmecophiles which apparently stay around the edges or base of the bivouac or in the refuse deposits. Included in this group are *Vatesus schneirlai*, the larvae of *V. panamensis*, Phoridae including *Ecitophora* spp. and *Thalloptera schwarzmaieri*, the histerid *Troglosternus ecitonis* and some of the staphylinids which are also seen at the beginning of the emigration.

Host Specificity of the Myrmecophiles: Most of the myrmecophiles found with Ecitonini are known from single hosts, but this apparently high degree of host specificity must be partially due to the small number of specimens in collections.

There are few cases where one species is found with hosts of two genera. For example, the histerid *Alloiodites* is known from *burchelli* and *praedator*, and this host relationship may be connected with the swarm raiding of both hosts. Another example, *Trichatelura borgmeieri*, has been found with four genera; but this thysanuran appears to be more abundant with *Nomamyrmex* and *Labidus* than with *Eciton* and *Neivamyrmex*. The discovery of rather large numbers of millipeds in colonies of *Labidus* and *Nomamyrmex* suggests a close phylogenetic relationship or similarity of behavior for the hosts. None of the myrmecophiles collected during this survey provide as much evidence as the millipeds to suggest relationships between any other two genera of army ants.

When the same species or two or more species within the same genus are found with different hosts, the ants are usually in the same genus. In most cases the myrmecophiles probably indicate a close phylogenetic relationship or similar behavior or habitats for the hosts. *Neivamyrmex nigrescens* and *opacithorax* have as myrmecophiles some of the same species of Phoridae and Staphylinidae. These ants are morphologically similar and have ranges which overlap. *Eciton vagans* and *dulcius crassinode* have several guests in common and also several found in addition with *mexicanum* or *hamatum*. *E. burchelli* appears to share more guests in common with *hamatum* than with any other host. The myrmecophiles found with the latter two pairs of hosts but not with others are more likely to indicate a close relationship between their hosts than the guests with *Neivamyrmex*, because the myrmecophiles with the five common species of *Eciton* were extensively collected on Barro Colorado Island. However, myrmecophiles may be found with *burchelli* and *hamatum* because these are the only primarily epigaeic army ants. Because the mites are much more abundant than the insects and can more readily be found in samples of ants from raid columns, the Acarina are best suited for a study of possible relationships among their hosts. Several generalizations can be made on the degree of host specificity for the various taxonomic groups of myrmecophiles. Most species of Diplopoda, Collembola and Thysanura and some Phoridae and Pyemotidae are found with more than one genus of army ants. The species of Acarina, Phoridae, Staphylinidae and Histeridae are each limited to one host with a few exceptions in each group.

Abundance of Myrmecophiles with Army Ants: Myrmecophiles are apparently more abundant both in numbers of species and individuals in colonies of *Labidus praedator* and *Nomamyrmex esenbecki* than in colonies of any other species of army ant. *Eciton burchelli* probably has the next largest number of myrmecophiles. Other species of *Eciton*, *Labidus* and *Nomamyrmex* have somewhat fewer and *Neivamyrmex* has the fewest species of guests.

Although I have not looked for myrmecophiles in as many colonies of nondoryline ants as in colonies of Ecitonini, it appears that any colony or species of army ant has a larger number of myrmecophilous species and individuals than most colonies or species of nondoryline ants. Consequently the tribe Ecitonini has a greater total number of myrmecophiles than any group of ants with the same approximate number of species. Brues (1902: 365) suggested that the doryline ants which he studied with Wheeler in Texas were "commonly seen to harbor a larger number and a greater range of myrmecophiles than any other restricted group of ants with which we are acquainted." My collecting in Kansas has been less thorough than that done by Wheeler and Brues in Texas, but more myrmecophiles were found in samples of Neivamyrmex than in samples of equal size from any other genus of nondoryline ants with the exception of an occasional colony heavily infested with a species of mite. Wheeler (1910: 386) also commented on the relative abundance of myrmecophiles in colonies of dorylines compared with those of nondoryline ants and have suggested that the large number of myrmecophiles may be a result of the abundance of booty in colonies of army ants.

The Dorylinae in the Eastern Hemisphere also have a large number of myrmecophiles, and the species are similar enough biologically that the factors which have contributed to the large numbers of myrmecophiles in the Ecitonini are probably the same for the entire subfamily.

I believe the abundance of myrmecophiles in colonies of army ants is due to the following factors: (1) A large amount of booty is constantly present, and at the beginning of the statary period there is a superabundance of booty within the bivouac. (2) The ants are almost exclusively carnivorous, and the majority of the species of myrmecophiles belong to the Histeridae and Staphylinidae which are primarily carnivorous or are scavengers on dead arthropods. Thus, the feeding habits of these guests required little or no modification when the beetles became myrmecophiles. (3) The colonies of army ants are exceptionally large compared with most nondoryline ants and other social insects except the termites. Consequently an adequate breeding population of a species of myrmecophile can live within a single colony without seriously depleting the food supply for the ants. Some termites and leafcutting ants have colonies equal to or exceeding the size of army ant colonies, and these other colonies also have large numbers or inquilines. A large colony size would also be an advantage for those myrmecophiles which feed on the surfaces of the ants, on the brood, or are parasitic on the ants. (4) Colonies of army ants are perpetual from the standpoint that new colonies start by a division of large colonies and can not be started like most colonies of ants by a single queen or by a queen with a small group of workers. Consequently, if inquilines can join a colony and accompany it when it emigrates, they and their offspring can avoid the hazards of periodically searching for and entering new colonies. (5) The doryline raid and emigration columns and their chemical trails are apparently more extensive than those of other ants making it easier for myrmecophiles to find colonies of army ants. (6) Having greatly reduced eyes, the army ants are not able to distinguish a myrmecophile from an ant by sight. It has been assumed by various authors that other ants attack myrmecophiles on the basis of visual discrimination, but I know of no experimental evidence to support this assumption. (7) Although the army ants have almost always been described as voracious predators killing all arthropods, these ants are specialized in their feeding and seem to be highly inefficient at killing arthropods much smaller than themselves. With a few exceptions the myrmecophiles are smaller than the workers of average size, and about 95% of the myrmecophiles (the Acarina, Collembola, Phoridae and Limulodidae) are minute. Although some non-doryline ants frequently kill prey much smaller than themselves, I know of no evidence that ants kill mites on their bodies; and it is impossible to state whether nondoryline ants kill their myrmecophiles more often than do doryline ants. (8) While the army ants were evolving, they lost compound eyes and apparently became more dependent upon chemoreceptors. The present behavior of the army ants is so highly dependent upon chemical trails and sensitivity to other chemicals that probably the Dorylinae are more sensitive to chemicals than most nondoryline ants. Based on this assumed hypersensitivity to chemicals, the Dorylinae are more likely than nondoryline ants to acquire myrmecophiles for the following reasons: (a) The army ants may not be able to distinguish myrmecophiles from worker ants if the guests can acquire the odor of the host's colony or species. (b) The army ants may be more sensitive to repellent chemicals. (c) The army ants may be more attracted to or pacified by secretions of the myrmecophiles.

The following groups of arthropods found in bivouacs or columns are listed here in order of decreasing abundance with the approximate number of specimens taken: Acarina (8,000), Phoridae (2,400), Limulodidae (1,100), Staphylinidae (300), Collembola (300), Thysanura (170), Diplopoda (150), Histeridae (140) and Diapriidae (6). From this list it can be seen that the myrmecophiles which are smallest in size are generally the most abundant. Within the Acarina the smallest mites, the Pyemotidae and Scutacaridae, were also most numerous. However, within the Limulodidae the genus Cephaloplectus, which includes the largest species, was more abundant than the small species.

Between 10 and 50 specimens of most of the larger common species of myrmecophiles appear to be present in a single colony of Eciton. However, it is clear that large fluctuations in populations are possible and much more collecting will be required before accurate estimates can be made of the populations of myrmecophiles within colonies. The Collembola and Pyemotidae had the highest populations within a colony with up to about one myrmecophile per four ants. The incidence of most common species of inquilines usually is between one per 500 and one per 10,000 ants. Of course some species were rare with only single specimens taken from samples totalling up to about 500,000 ants.

Life Cycles of the Myrmecophiles: I know of no myrmecophile found with the army ants which has been reared from the immature to the adult stage. Few immature stages have been found within bivouacs or columns. Most immature stages which have been taken cannot be associated with adults. Because most larvae of Diptera and Coleoptera have been found in refuse deposits, these larvae more likely belong to the adults which are common in the refuse deposits rather than to the myrmecophilous species found within bivouacs.

Larvae, nymphs and adults of *Laelaspis* (Laelaptidae) have been found within the same sample of ants, indicating that this mite probably breeds continuously within the colonies. No similar series of instars for any other mite or insect was found at any one time in a colony.

Collecting data for two species suggest that the life cycles of some of the myrmecophilous insects are correlated with the nomadic-statary cycle of their hosts. Nymphs of *Trichatelura manni* (Thysanura) and larvae of *Vatesus panamensis* (Staphylinidae) were found primarily at the beginnings of nomadic phases. Eggs are probably deposited at the beginning of the statary phase when booty would be most abundant in the colony. Because *Vatesus* has an inactive prepupal and pupal stage, either the ants must carry these stages, or after pupation in the ground the adults must re-enter colonies. The presence of well-developed wings on _V_. _panamensis_ supports the latter hypothesis. A number of larvae of _V_. _panamensis_ were reared to prepupae, and one was reared to the pupal stage, but all specimens died or were killed by mites before reaching the adult stage. No prepupae or pupae were ever found in or near colonies.

At least one species of pyemotid mite and a new family of mesostigmate mites, which when gravid look like ant larvae, have life cycles probably correlated with the nomadic-statary cycle. In addition, there is a little evidence suggesting that the life cycle of several species of related mites (probably in the family Neoparasitidae) have life cycles correlated with the production of sexual broods of the ants. The females have been found on male ants taken at lights, and the male mites were found at the times when the male ants are produced. The females of the mites are in the colonies throughout the year.

Food of the Myrmecophiles: Any attempt at classifying myrmecophiles on the basis of their food is almost impossible because each species probably eats a variety of substances. The guests usually feed for a few seconds or less at any one place, making it difficult to observe how they are feeding or what they are eating. At the present time the myrmecophiles found with army ants can be divided into the following groups according to what are thought to be their most common feeding habits: (1) endoparasites, (2) ectoparasites, (3) strigilators and surface feeders, (4) trophallactic feeders, (5) predators on booty and brood, (6) predators on adult workers and (7) scavengers.

Some of the Phoridae with heavily sclerotized ovipositors are considered to be endoparasites of the army ants, but as far as I can determine none of the species has been reared. No information on the biology or behavior of these species was gathered during my work.

No ectoparasitic insects are known from army ants, but a large number of mites have been shown or are assumed to feed on the brood or adult ants. Mites which are known to insert their mouthparts into the adults are Macrochelidae, Neoparasitidae and Pyemotidae. The Neoparasitidae and Circocyllibanidae are ectoparasites on the ant larvae, and the following groups probably have the same feeding habits: Parasitoidea nymphs, Macrochelidae, Laelaptidae, Uropodina and Pyemotidae.

A large group of myrmecophiles feeds on material licked or scraped from the surfaces of adult and larval ants. Thysanura (Trichatelura), Collembola, Limulodidae and some Staphylinidae and Histeridae are in this group. Insects in all the groups listed (except the Collembola?) were seen strigilating (rapidly scraping with any of the mouthparts) and also licking (touching with their maxillae or labia) the surfaces of ants. The first three groups are considered primarily strigilators. The collembolan Cyphoda which might be expected to feed on fungi or mold in refuse deposits was never found there but was abundant in samples of larvae on which it apparently fed.

Two species of Euxenister apparently are trophallactic feeders, because they were seen to stop workers and place their mouthparts against those of the ants. No fluid could be seen around the mouthparts, and there is no proof that any substance was exchanged.

All the insect families and orders listed above as strigilators feed on liquids oozing from injured booty and brood. However, some histerids and mites pierce uninjured larvae and booty. I believe the behavior of these histerids and mites may be important for initiating feeding on the brood by the other myrmecophiles and the army ants. *Vatesus panamensis* was not seen strigilating and probably did not puncture any booty or brood but was seen feeding on fluids oozing from them.

The staphylinid *Tetradonia marginalis* is the only myrmecophile positively shown to attack active workers. However, this species, two other species of *Tetradonia* and at least two species of *Zyras s. lat.* were seen to attack workers which were unable to walk but still were twitching. Possibly these beetles are actually predators which killed the ants.

The staphylinids which attack active workers also feed on dead workers, and therefore can be considered scavengers as well as predators. In addition, the myrmecophilous scavengers should include at least those species which feed on booty refuse and follow the emigrations of the ants. Most Phoridae and some of the Staphylinidae and Histeridae which show no obvious morphological specializations for myrmecophily are scavengers. The Diplopoda are known to feed on dirt and debris (but not booty refuse) in laboratory nests and are thought to be scavengers around the bivouacs of the ants. *Vatesus* spp. which usually stay within the bivouacs occasionally visit refuse deposits and feed on the remains of booty.

Other Behavior of the Myrmecophiles: This study showed that the classical division of myrmecophiles into symphiles, synoeketes and synechthrans proposed by Wasmann is of little or no value for referring to the guests of the army ants. Species long considered by authors to be symphiles are apparently ignored or killed as readily as species reported to be persecuted predators (synechthrans).

Most species which appear to be carried by the ants were shown to climb up to the undersides of the heads of workers where they actually ride. Although some species are actively carried by the ants, the importance of this behavior seems to have been overstressed in the past. In addition to their booty and brood, the army ants in emigration columns also carry living and uninjured workers of their colony, empty cocoons, sclerites from booty lacking any apparent food, and even pieces of dirt and wood. It seems doubtful that many of the morphological features such as the large curved legs or the dorsolateral carinae considered to be "handles" are adaptations for being carried by the workers. Over 50 specimens of some of these species were seen running or riding in emigration columns, but I did not see a single individual being carried by an ant. The staphylinid Mimonilla ?ecitonis was the species most consistently carried in an emigration column and laboratory nest.

All species of Diplopoda and Phoridae seen in columns were running, and these inquilines never rode on the ants in laboratory nests. Most species of Collembola, Thysanura, Staphylinidae and Histeridae either ride or run in the columns. The largest species of Vatesus (Staphylinidae) and the adult Trichatelura (Thysanura) rarely ride. Although even Collembola and the smallest species of Limulodidae were seen to run in emigration columns, these small species commonly rode on the ants or whatever the ants were carrying. As the ant larvae increase in size, a larger proportion of all the myrmecophiles ride on the brood. Some species of Histeridae and many of the mites ride on specific places on the worker ants, and some ride only on major or submajor workers.

Every species of myrmecophile tested was able to follow the chemical trails of its host when no ants were on the trail. Included were such diverse groups as Diplopoda, Collembola, Thysanura, Phoridae, Limulodidae, Staphylinidae and Histeridae.

Any long hairs arranged in groups and usually yellow in color have been considered by most authors to be trichomes bearing a substance virtually irresistible to the ants. It has been claimed that this substance not only protects the insects from being killed by their hosts but induces the ants to carry and care for the myrmecophiles. The ants were not attracted to the trichomes and licked other parts of _Euxenister_ rarely but more than they licked the trichomes. The main function of the trichomes may be to remove and hold material from the surfaces of the ants. However, the dorsal trichome hairs may be of some protective advantage because they will break off if an ant pulls on them. Moreover, the long hairs on the tibiae of histerids such as _Euxenister_ are on the inner surfaces where the hairs clearly increase the efficiency of the legs used by the histerid to alternately rub the workers and its own body. This rubbing process occurs frequently and may be important for transferring the colony odor from the bodies of the ants to the beetles. It is also possible that the glands associated with the trichomes produce a substance which absorbs chemicals from the surfaces of the ants allowing the histerid to acquire the odor of the colony. In addition to two species of _Euxenister_, the staphylinid _Ecitophya bicolor_ was seen rubbing its legs on the bodies of workers and then on its own body. This staphylinid does not have hairs as extensively developed on its legs as does the histerid.

None of the myrmecophiles seen climbing, kicking or scraping on the surfaces of the ants was ever attacked by the workers (except for a few histerids which were clinging to heads of workers and had their mouthparts touching those of the workers). Even large beetles clinging to legs or antennae were not attacked, and myrmecophiles were never seen in balanced positions on the ants. When myrmecophiles climbed on the queens, the workers made no attempt to remove the inquilines even though the workers themselves usually ride and cluster around the queen. In some cases the workers were completely displaced by the myrmecophiles. Some limulodids and occasionally Vatesus and Trichatelura were the only myrmecophiles which appeared to be more attracted to queens than to workers.

The methods and extent of dispersal from one colony to another are unknown except for some Laelaptidae and Neoparasitidae which are known to ride on male army ants. These mites were found on males which had flown to lights, and I suspect that this method of dispersal may be used by a number of other families of mites and the smallest myrmecophilous beetles.

V. LITERATURE CITED

Aldrich, J. M. 1929. Further studies of types of American muscoid flies in the collection of the Vienna Natural History Museum. Proc. U. S. Nat. Mus., 74(19): 1-34.

1930. American two-winged flies of the genus Stylogaster Macquart. Proc. U. S. Nat. Mus., 78(9): 1-27.

Allee, W. C. 1926a. Measurement of environmental factors in the tropical rain-forest of Panama. Ecology, 7: 273-302.

1926b. Distribution of animals in a tropical rain-forest with relation to environmental factors. Ecology, 7: 445-468.

Baker, E. W., J. H. Camin, F. Cunliffe, T. A. Woolley and C. E. Yunker. 1958. Guide to the families of mites. Contr. No. 3, Inst. Acarology, Univ. Maryland. ix + 242 p.

Baker, E. W., and G. W. Wharton. 1952. An introduction to acarology. New York: Macmillan. xiii + 465 p.

Bates, H. W. 1863. The naturalist on the River Amazons. London: John Murray. vol. 1: viii + 351 p., 1 map; vol. 2: vi + 423 p.

Beard, J. S. 1944. Climax vegetation in tropical America. Ecology, 25: 127-158.

1955. The classification of tropical American vegetation-types. Ecology, 36: 89-100.

Beebe, W. 1917. With army ants "somewhere" in the jungle. Atlantic Monthly, 119: 514-522.

1919. The home town of the army ants. Atlantic Monthly, 124: 454-464.

Beneway, D. F. 1960. Androeuryops, a new genus of Tachinidae (Diptera) from Central America. Jour. Kansas Ent. Soc., 34: 44-47.

Bequaert, J. C. 1922. The predaceous enemies of ants. Bull. Amer. Mus. Nat. Hist., 45: 271-332, pl. 1, 24-25.

1930. Are ants better protected against the attacks of their predaceous enemies than other arthropods? Zool. Anz., 88: 163-176.

Berlese, A. 1903. Diagnosi di alcune nuove specie di Acari italiani, mirmecofili e liberi. Zool Anz., 27: 12-28.

1904a. Acari nuovi. Manipulus I. Redia, 1: 235-252.

1904b. Illustrazione iconografica degli Acari mirmecofili. Redia, 1: 299-474, pl. 7-20.

Borgmeier, T. 1928. Investigações sôbre phorideos myrmecophilos (Diptera, Phoridae). Arch. Inst. Biol. (Def. Agric. Anim.), 1: 159-192, pl. 27-35.

1931. Um cypselideo ecitophilo de Goyaz (Dipt., Cypselidae). Rev. Ent., S. Paulo, 1: 30-37, pl. 1.

1933. A rainha de Eciton rogeri Dalla Torre (Hym. Formicidae). Rev. Ent., Rio de Janeiro, 3: 92-96.

1935. Sobre alguns Cynipideos parasiticos e cecidogenos do Brasil. (Hymenoptera, Cynipidae). Arch. Inst. Biol. Veg., Rio de Janeiro, 2: 97-124, pl. 1-6.

1939. Sobre alguns Diapriideos myrmecophilos, principalmente do Brasil (Hym. Diapriidae). Rev. Ent., Rio de Janeiro, 10: 530-545.

1948a. Die Geschlechtstiere zweier Eciton-Arten und einige andere Ameisen aus Mittel- und Suedamerika (Hym. Formicidae). Rev. Ent., Rio de Janeiro, 19: 191-206.

1948b. Zur Kenntnis der bei Eciton lebenden myrmekophilen Histeriden (Col.). Rev. Ent., Rio de Janeiro, 19: 378-400.

1949. Neue Arten und Gattungen ecitophiler Staphyliniden, nebst einem Katalog aller bisher beschriebenen Arten. (Col. Staph.) Rev. Ent., Rio de Janeiro, 20: 93-158.

1953. Vorarbeiten zu einer Revision der Neotropischen Wanderameisen (Hym. Formicidae). Studia Ent., s. 1, no. 2: 1-51.

1954. Eine neue myrmekophile Dipterengattung aus Brasilien. Zool. Anz., 153: 292-298.

1955. Die Wanderameisen der Neotropischen Region (Hym. Formicidae). Studia Ent., s. 1, no. 3: 1-716, pl. 1-87.

1956. Revision der ecitophilen Gattung "Mimophites" Fauvel, nebst Beschreibung einer neuen Gattung aus Bolivien (Coleoptera, Staphylinidae). Rev. Bras. Biol., 16: 1-16.

1958a. Nachtraege zu meiner Monographie der neotropischen Wanderameisen (Hym. Formicidae). Studia Ent., (2)1: 197-208.

1958b. Neue Beitraege zur Kenntnis der ecitophilen Staphyliniden (Col.). Studia Ent., (2)1: 225-246.

1958c. Aparelho simples para captura de insetos ecitofilos. Studia Ent., (2)1: 290.

1959. Nota prévia sôbre alguns coleópteros ecitófilos da familia Staphylinidae. Bol. Mus. Nac., Rio de Janeiro, n. s., Zoologia, no. 214: 1-15.

Borgmeier, T., and H. Schmitz. 1923. Beitrag zur Kenntnis der Phoriden Brasiliens. Z. Dtsch. Ver. Wiss., S. Paulo, 3: 127-148, pl. 11.

Brauer, F., and J. E. Bergenstamm. 1891-1893. Die Zweiflügler des Kaiserlichen Museums zu Wien. Parts 5-6. Vorarbeiten zu einer Monographie der Muscaria schizometopa - exclusive Anthomyidae. Denkschr. Akad. Wiss. Wien, Math. - nat. Kl.

Brian, M. V. 1958. The evolution of queen control in the social Hymenoptera. Proc. 10th Int. Congr. Ent., Montreal, 1956, 2: 497-502.

Brown, W. L. 1960. The release of alarm and attack behavior in some New World army ants. Psyche, Camb., Mass., 66: 25-27.

Bruch, C. 1919. Un nuevo coleóptera ecitófilo. Physis, Buenos Aires, 4: 579-582.

1923. Estudios mirmecologicos. Rev. Mus. La Plata, 27: 172-220, pl. 1-6.

1926a. Coleópteros mirmecófilos de Córdoba. Rev. Soc. Ent. Argent., 1(2): 3-12, 1 pl.

1926b. Nuevos Histéridos ecitófilos (Col.). Rev. Mus. La Plata, 29: 17-33, pl. 1-2.

1928. Estudios mirmecológicos. An. Mus. Nac. Hist. Nat., 34: 341-360, 6 pl.

1929. Neue myrmecophile Histeriden und Verzeichnis der aus Argentinien bekannten Ameisengaeste. Zool. Anz., 82: 421-437.

1931. Algunos mirmecófilos y termitófilos nuevos y poco conocidos de la Argentina. Rev. Ent., S. Paulo, 1: 387-395, pl. 2.

1934a. Las formas femeninas de *Eciton*. Descripcion y redescripcion de algunas especies de la Argentina. An. Soc. Cient. Argent., 118: 113-135, pl. 1-3.

1934b. Breves observaciones sobre costumbres de *Eciton* (*Holopone*) *dulcius* For. var. *jujuyensis* For. y descripcion del macho (Hym. Formic.). Rev. Soc. Ent. Argent., 6: 261-265, pl. 25.

Brues, C. T. 1901. Two new myrmecophilous genera of aberrant Phoridae from Texas. Amer. Nat., 35: 337-356.

1902. New and little-known guests of the Texan legionary ants. Amer. Nat., 36: 365-378.

Calvert, A. S., and P. P. Calvert. 1917. A year of Costa Rican natural history. New York: Macmillan. xix + 577 p.

Camras, S. 1955. New Conopidae from South America, Africa, and Australia (Diptera). Ent. News, 66: 119-125.

1958. Descriptions and records of Neotropical Conopidae (Diptera). Psyche, Camb., Mass., 64: 9-16 (1957).

Carpenter, G. D. H. 1915. Dr. G. D. H. Carpenter's observations on *Dorylus nigricans*, Illig., in Damba and Bugalla Islands. Proc. Ent. Soc. London, 1914: cvii-cxi.

Caudell, A. N. 1925. A new species of myrmecophilous Thysanura from Bolivia. Proc. Ent. Soc. Wash., 27: 43-45.

Causey, N. B. 1960. Millipeds collected in Guatemalan caves, including *Calymmodesmus inguinatus*, n. sp. (Stylodesmidae: Polydesmida). Proc. Biol. Soc. Wash., 73: 275-280.

Chamberlin, R. V. 1938. Diplopoda from Yucatan. Carnegie Inst. Wash. Pub. No. 491: 165-182.

1947. A new myrmecophilous milliped from Mexico. Pan-Pacific Ent., 23: 101-102.

Chapman, F. M. 1929. My tropical air castle. New York: Appleton-Century. xv + 417 p.

1938. Life in an air castle. New York: Appleton-Century. xii + 250 p.

Chillcott, J. G. 1958. Two new species of *Euryomma* (Stein) (Muscidae: Diptera) from Panama. Canadian Ent., 90: 725-731.

Clausen, C. P. 1940. Entomophagous insects. New York: McGraw-Hill. x + 688 p.

Cohic, F. 1948. Observations morphologiques et écologiques sur Dorylus (Anomma) nigricans Illiger. Rev. Franc. Ent., 14 (suppl.): 229-276.

Cole, A. C. 1953. Studies of New Mexico ants. III. The ponerines and dorylines (Hymenoptera: Formicidae). Jour. Tenn. Acad. Sci., 28: 84-85.

Collart, A. 1934. Notes de chasse au sujet de quelques Coléoptères du Congo Belge. Bull. (Ann.) Soc. Ent. Belg., 74: 230-250.

Cook, O. F. 1896. Summary of new Liberian Polydesmoidea. Proc. Acad. Nat. Sci. Philadelphia, 1896: 257-267.

Coquillett, D. W. 1910. The type species of the North American genera of Diptera. Proc. U. S. Nat. Mus., 37: 499-647.

Creighton, W. S. 1950. The ants of North America. Bull. Mus. Comp. Zool., Harvard, 104: 1-587, 57 pl.

Curran, C. H. 1934a. Review of the tachinid genus Calodexia van der Wulp (Diptera). Amer. Mus. Novit., no. 685: 1-21.

1934b. The Diptera of Kartabo, Bartica district, British Guiana, with descriptions of new species from other British Guiana localities. Bull. Amer. Mus. Nat. Hist., 66: 287-532.

1934c. The families and genera of North American Diptera. New York: Ballou Press. 512 p., 2 pl.

1942. American Diptera. Bull. Amer. Mus. Nat. Hist., 80: 51-84.

Delamare-Deboutteville, C. 1947. Facteurs écologiques et éthologiques dans l'étude des Collemboles termitophiles et myrmécophiles (Note préliminaire). Bull. Mus. Hist. Nat., Paris, (2)19: 456-458.

1948. Recherches sur les collemboles termitophiles et myrmécophiles (écologie, éthologie, systématique). Arch. Zool. Exp. Gén., Paris, 85: 261-425.

Donisthorpe, H. St. J. K. 1927. The guests of British ants: their habits and life-histories. London: George Routledge. xxiii + 244 p.

Duda, O. 1924. *Aptilotella Borgmeieri* ♂, eine neue flügellose Borboride (Dipt.) aus Brasilien. Natuurhist. Maandbl., Maastricht, 13: 74-76.

Eidmann, H. 1936. Oekologisch-faunistische Studien an suedbrasilianischen Ameisen. Arb. Physiol. Angew. Ent. Berlin, 3: 26-112, 1 pl.

Eisner, T. 1957. A comparative morphological study of the proventriculus of ants (Hym.: Formicidae). Bull. Mus. Comp. Zool., Harvard, 116: 439-490, 25 pl.

Eisner, T., and W. L. Brown, Jr. 1958. The evolution and social significance of the ant proventriculus. Proc. 10th Int. Congr. Ent., Montreal, 1956, 2: 503-508.

Emden, F. I. van. 1947. Keys to the Ethiopian Tachinidae. II. Dexiinae. Proc. Zool. Soc. London, 116: 627-674, pl. 1-3.

Enders, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panama. Bull. Mus. Comp. Zool., Harvard, 78: 385-502, pl. 1-5.

Escherich, K. 1905. Das System der Lepismatiden. Zoologica, Stuttgart, 18(43): 1-164, pl. 1-4.

Fage, L. 1938. Quelques arachnides provenant de fourmilières ou de termitières du Costa Rica. Bull. Mus. Hist. Nat., Paris, (2)10: 369-376.

Ferrière, C. 1929. Nouveaux Diapriides du Brésil, hôtes des *Eciton*. Zool. Anz., 82: 156-171.

Fiebrig, K. 1907a. Eine Wespen zerstörende Ameise aus Paraguay, *Eciton vagans* Olivier. Z. Wiss. Insektenbiol., 3: 83-87.

1907b. Nachtrag zu: Eine Wespen zerstörende Ameise aus Paraguay. Z. Wiss. Insektenbiol., 3: 154-156.

Fitch, H. S. 1952. The University of Kansas Natural History Reservation. Univ. Kansas Mus. Nat. Hist. Misc. Publ. no. 4: 1-38, 4 pl.

Hagan, H. R. 1954a. The reproductive system of the army-ant queen, *Eciton* (*Eciton*). Part 1. General anatomy. Amer. Mus. Novit., no. 1663: 1-12.

1954b. The reproductive system of the army-ant queen, *Eciton* (*Eciton*). Part 2. Histology. Amer. Mus. Novit., no. 1664: 1-17.

1954c. The reproductive system of the army-ant queen, *Eciton* (*Eciton*). Part 3. The oöcyte cycle. Amer. Mus. Novit., no. 1665: 1-20.

Hall, D. G. 1948. The blowflies of North America. Thomas Say Foundation. 477 p., 51 pl.

Holmgren, N. 1908. Ueber einige myrmecophile Insekten aus Bolivia und Peru. Zool. Anz., 33: 337-349.

Howell, T. R. 1957. Birds of a second-growth rain forest area of Nicaragua. Condor, 59: 73-111, 1 pl.

Ihering, H. von. 1894. Die Ameisen von Rio Grande do Sul. Berl. Ent. Z., 39: 321-446, 1 pl.

1912. Biologie und Verbreitung der brasilianischen Arten von *Eciton*. Ent. Mitt., 1: 226-235.

Jackson, W. B. 1957. Microclimatic patterns in the army ant bivouac. Ecology, 38: 276-285.

Janet, C. 1896. Sur les rapports des Lépismides myrmécophiles avec les fourmis. Comptes Rendus Acad. Sci., 122: 799-802.

1897. Rapports des animaux myrmécophiles avec les fourmis. Études sur les fourmis, les guêpes et les abeilles. Note 14. Limoges: Ducourtieux. 99 p.

Jeannel, R. 1956. Les Psélaphides myrmécophiles de l'Afrique Intertropicale. Rev. Franc. Ent., 23: 197-215.

Johnson, R. A. 1954. The behavior of birds attending army ant raids on Barro Colorado Island, Panama Canal Zone. Proc. Linn. Soc. N. Y., no. 63-65: 41-70 (1951-1953).

Kenoyer, L. A. 1929. General and successional ecology of the lower tropical rain-forest at Barro Colorado Island, Panama. Ecology, 10: 201-222.

Klots, A. B., and E. B. Klots. 1959. Living insects of the world. New York: Chanticleer Press. 304 p.

Kröber, O. 1940. Beiträge zur Kenntnis der Conopiden. V. Ann. Mag. Nat. Hist., (11)5: 64-82.

Kullback, S. 1959. Information theory and statistics. New York: Wiley. xvii + 395 p.

Lamborn, W. A. 1914a. Mr. W. A. Lamborn's observations on the driver ants (Dorylus) of Southern Nigeria. Proc. Ent. Soc. London, 1913: cxxiii-cxxviii.

1914b. W. A. Lamborn's further notes on the driver ants (Dorylus) of Southern Nigeria. Proc. Ent. Soc. London, 1914: v-viii.

1920. Further notes by W. A. Lamborn on the habits of the fly Bengalia. Proc. Ent. Soc. London, 1919: lii-lviii.

Lindquist, A. W. 1942. Ants as predators of Cochliomyia americana

C. & P. Jour. Econ. Ent., 35: 850-852.

Loomis, H. F. 1959. New myrmecophilous millipeds from Barro Colorado Island, Canal Zone, and Mexico. Jour. Kansas Ent. Soc., 32: 1-7.

1961. New and previously known millipeds of Panama. Proc. U. S. Nat. Mus., 113: 77-124.

Lopes, H. Souza. 1937. Contribução ao conhecimento do gênero "Stylogaster." Arch. Inst. Biol. Veg., Rio de Janeiro, 3: 257-293.

1938. Sôbre uma nova espécie do gênero Stylogaster Macquart, do Brasil (Dipt.: Conopidae). Mem. Inst. Osw. Cruz, 33: 403-405, pl. 1.

1946. Contribução ao conhecimento das espécies do gênero Notochaeta Aldrich, 1916 (Diptera-Sarcophagidae). Mem. Inst. Osw. Cruz, 42: 503-550.

Lopes, H. de Souza, and L. Monteiro. 1959. Sôbre algumas espécies brasileiras de Stylogaster Macquart, com a descrição de quatro espécies novas (Diptera, Conopidae). Studia ent., (2)2: 1-24.

Luederwaldt, H. 1918. Notas myrmecologicas. Rev. Mus. Paulista, São Paulo, 10: 31-64, 1 pl.

Mann, W. M. 1925. Guests of Eciton hamatum (Fab.) collected by Professor W. M. Wheeler. Psyche, Camb., Mass., 32: 166-177.

1948. Ant hill odyssey. Boston: Little, Brown. 338 p.

Meijere, J. C. H. de. 1904. Beiträge zur Kenntniss der Biologie und der systematischen Verwandtschaft der Conopiden. Tijdschr. Ent., 46: 144-225, pl. 14-17.

Mello-Leitão, M. 1925. Dois interessantes arachnideos myrmecophilos. Physis, Buenos Aires, 8: 228-237.

1926. Algumas aranhas do Brasil Meridional. Bol. Mus. Nac. Rio de Janeiro, 2(5): 1-18.

Mellor, J. E. M. 1922. Notes on a Bengalia-like fly, which I have called the "Highwayman" fly, and its behaviour towards certain species of ants. Sudan Notes Records, 5: 95-100.

Michener, C. D., and M. H. Michener. 1951. American social insects. New York: Van Nostrand. xiv + 267 p.

Moniez, R. 1895. Sur quelques Arthropodes trouvés dans des fourmilières. Rev. Biol. N. Fr., 6: 201-215.

Moynihan, M. H. 1959. General information concerning facilities for study at Canal Zone Biological Area (Barro Colorado Island). Turtox News, 37: 2-5.

Muesebeck, C. F. W., et al. 1951. Hymenoptera of America north of Mexico. Synoptic catalog. U. S. Dept. Agr., Agr. Monogr. No. 2: 1420 p.

Nesbitt, H. H. J. 1945. A revision of the family Acaridae (Tyroglyphidae), order Acari, based on comparative morphological studies. Part I. Historical, morphological, and general taxonomic studies. Canadian Jour. Res., (D)23: 139-188.

Park, O. 1929. Ecological observations upon the myrmecocoles of Formica ulkei Emery, especially Leptinus testaceus Mueller. Psyche, Camb., Mass., 36: 195-215.

1933. Ecological study of the ptiliid myrmecocole, Limulodes paradoxus Mathews. Ann. Ent. Soc. Amer., 26: 255-261.

1942. A study in Neotropical Pselaphidae. Northwestern Univ. Stud. Biol. Sci. Med., 1: x + 403 p., 21 pl.

Paulian, R. 1948. Observations sur les Coléoptères commensaux d'Anomma nigricans en Côte d'Ivoire. Ann. Sci. Nat., Zool., (11)10: 79-102.

Pohl, L. 1957. Vergleichende anatomisch-histologische Untersuchungen an *Lepisma saccharina* Linné und der Myrmecophilen *Atelura formicaria* Heyden (Beitrag zur Myrmecophilie, erster Abschnitt). Insectes Sociaux, 4: 349-363.

Radford, C. D. 1950. Systematic check list of mite genera and type species. Un. Int. Sci. Biol., Paris, (C)1: 1-232.

Raffray, A. 1909. Nouvelles espècies de Psélaphides. Ann. Soc. Ent. Fr., 78: 15-52.

Raignier, A. 1959. Het Ontstaan van Kolonies en Koninginnen bij de Afrikaanse Trekmieren. Meded. Vlaamsche Acad. Kl. Wet., 21(2): 1-24.

Raignier, A., and J. van Boven. 1955. Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera, Formicidae). Ann. Mus. R. Congo Belge, Terveren, n. s., Sci. Zool., 2: 1-359.

Reh, L. 1897. Biologische Beobachtungen an brasilianischen Ameisen. Ill. Wschr. Ent., 2: 600-603, 612-616.

Reichensperger, A. 1923a. Neue südamerikanische Histeriden als Gäste von Wanderameisen und Termiten. Mitt. Schweiz. Ent. Ges., 13: 313-336, pl. 13.

1923b. Neue südamerikanische Histeriden als Gäste von Wanderameisen und Termiten. I. Systematischer Teil. Z. Wiss. Insektenbiol., (2)18: 243-252, pl. 3.

1924a. Neue südamerikanische Histeriden als Gäste von Wanderameisen und Termiten. II. Teil. Rev. Suisse Zool., 31: 117-152, 1 pl.

1924b. Das Weibchen von *Eciton quadriglume* Hal., einige neue ecitophile Histeriden und allgemeine Bemerkungen. Zool. Anz., 60: 201-213.

1926. Neue Beiträge zur Artenkenntnis und zur Lebensweise myrmecophiler Histeriden. Verh. III. Int. Ent. Kongr., Zürich, 1925, 2: 184-203.

1929. Systematische und ökologische Myrmekophilen-Beiträge (Staphyl., Hist., Pauss.). Zool. Anz., 82: 257-268.

1932. Ecitophilen und Termitophilen aus Costa Rica (1), nebst Bemerkungen über fühlerbildung bei *Mimeciton* (Col. Hist. Staph.). Rev. Ent., S. Paulo, 2: 6-14.

1933a. Ecitophilen aus Costa Rica (II), Brasilien und Peru (Staph. Hist. Clavig.). Rev. Ent., Rio de Janeiro, 3: 179-194, pl. 3.

1933b. Neue ecitophile Histeriden aus Mittel- und Südamerika. Zool. Anz., 101: 299-309.

1934. Beitrag zur Kenntnis von *Eciton lucanoides* Em. Zool. Anz., 106: 240-245.

1935. Beitrag zur Kenntnis der Myrmekophilenfauna Brasiliens und Costa Ricas III. Arb. Morph. Taxon. Ent., Berlin, 2: 188-218, 1 pl.

1936. Beitrag zur Kenntnis der Myrmecophilen- und Termitophilenfauna Brasiliens und Costa Ricas. IV. (Col. Hist. Staphyl. Pselaph.). Rev. Ent., Rio de Janeiro, 4: 222-242, 1 pl.

1938. Beiträge zur Kenntnis der Myrmecophilen- und Termitophilenfauna Brasiliens und Costa Ricas. V. (Col. Hist. Staph.). Rev. Ent., Rio de Janeiro, 9: 74-97, pl. 2.

1939a. Beiträge zur Kenntnis der Myrmecophilen- und Termitophilenfauna Brasiliens und Costa Ricas. VI. (Col. Hist. Staph.). Rev. Ent., Rio de Janeiro, 10: 97-137.

1939b. Beiträge zur Kenntnis der Myrmecophilenfauna Costa Ricas und Brasiliens VII, nebst Beschreibung der Königin von *Eciton*

(Acamatus) pilosum. Zool. Jb., Syst., 73: 261-300.

Remington, C. L. 1954. The suprageneric classification of the order Thysanura (Insecta). Ann. Ent. Soc. Amer., 47: 277-286.

Richards, O. W. 1930. The British species of Sphaeroceridae (Borboridae, Diptera). Proc. Zool. Soc. London, 1930: 261-345, pl. 1.

1950. New species of Sphaeroceridae (Diptera) found with driver ants (Dorylinae) by S. Patrizi and F. Meneghetti. Boll. Ist. Ent. Univ. Bologna, 18: 14-23.

1951. New species of the genus "Safaria" Richards and of "Sphaerocera" Latreille (Dipt., Sphaeroceridae.). Boll. Ist. Ent. Univ. Bologna, 18: 268-271.

Roback, S. S. 1951. A classification of the muscoid calyptrate Diptera. Ann. Ent. Soc. Amer., 44: 327-361.

Schiner, I. R. 1868. Reise der österreichischen Fregatte Novara um die Erde in den Jahre 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. Zool. Theil. Bd. 2, Diptera. Wien: K. Gerold's Sohn. vi + 390 p.

Schneirla, T. C. 1933. Studies on army ants in Panama. Jour. Comp. Psychol., 15: 267-299.

1934. Raiding and other outstanding phenomena in the behavior of army-ants. Proc. Nat. Acad. Sci., Wash., 20: 316-321.

1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. Jour. Comp. Psychol., 25: 51-90.

1940. Further studies on the army-ant behavior pattern. Mass organization in the swarm-raiders. Jour. Comp. Psychol., 29: 401-460.

1944a. A unique case of circular milling in ants, considered in relation to trail following and the general problem of orientation. Amer. Mus. Novit., no. 1253: 1-26.

1944b. Studies on the army-ant behavior pattern. Nomadism in the swarm-raider Eciton burchelli. Proc. Amer. Philos. Soc., 87: 438-457.

1944c. The reproductive functions of the army ant queen as pacemakers of the group behavior pattern. Jour. N. Y. Ent. Soc., 52: 153-192.

1945. The army-ant behavior pattern: nomad-statary relations in the swarmers and the problem of migration. Biol. Bull., 88: 166-193.

1947. A study of army-ant life and behavior under dry-season conditions with special reference to reproductive functions. 1. Southern Mexico. Amer. Mus. Novit., no. 1336: 1-20.

1948. Army-ant life and behavior under dry-season conditions with special reference to reproductive functions. II. The appearance and fate of the males. Zoologica, N. Y., 33: 89-112, 1 pl.

1949a. Problems in the environmental adaptation of some new-world species of doryline ants. Anal. Inst. Biol. Mex., 20: 1-14.

1949b. Army-ant life and behavior under dry-season conditions. 3. The course of reproduction and colony behavior. Bull. Amer. Mus. Nat. Hist., 94: 1-82, 2 pl.

1952. Basic correlations and coordinations in insect societies with special reference to ants. Colloq. Int. Cent. Nat. Rech. Sci., 34: 247-269.

1953. The army-ant queen: keystone in a social system. Bull. Union Int. Étude Ins. Sociaux, 1: 29-41.

1956a. A preliminary survey of colony division and related processes in two species of terrestrial army ants. Insectes Sociaux, 3: 49-69.

1956b. The army ants. Rep. Smithson. Inst., 1955: 379-406, 2 pl.

1957a. Theoretical consideration of cyclic processes in doryline ants. Proc. Amer. Philos. Soc., 101: 106-133.

1957b. A comparison of species and genera in the ant subfamily Dorylinae with respect to functional pattern. Insectes Sociaux, 4: 259-298.

1958. The behavior and biology of certain nearctic army ants. Last part of the functional season, southeastern Arizona. Insectes Sociaux, 5: 215-255.

1961. The behavior and biology of certain nearctic doryline ants. Sexual broods and colony division in Neivamyrmex nigrescens. Z. f. Tierpsychology, 18: 1-32.

Schneirla, T. C., and R. Z. Brown. 1950. Army-ant life and behavior under dry-season conditions. 4. Further investigation of cyclic processes in behavioral and reproductive functions. Bull. Amer. Mus. Nat. Hist., 95: 263-354, 1 pl.

1952. Sexual broods and the production of young queens in two species of army ants. Zoologica, N. Y., 37: 5-32, 3 pl.

Schneirla, T. C., R. Z. Brown and F. C. Brown. 1954. The bivouac or temporary nest as an adaptive factor in certain terrestrial species of army ants. Ecol. Monogr., 24: 269-296.

Schneirla, T. C., and J. S. Rosenblatt. 1961. Behavioral organization and genesis of the social bond in insects and mammals. (Animal Research Panel, 1960). Amer. Jour. Orthopsychiatry, 31: 223-253.

Schubart, 1953

Seevers, C. H. 1958. A revision of the Vatesini, a tribe of Neotropical myrmecophiles (Coleoptera, Staphylinidae). Rev. Bras. Ent., S. Paulo, 8: 181-202, 3 pl.

1959. North American Staphylinidae associated with army ants. Coleop. Bull. 13: 65-79.

Seevers, C. H., and H. S. Dybas. 1943. A synopsis of the Limulodidae (Coleoptera): a new family proposed for myrmecophiles of the subfamilies Limulodinae (Ptiliidae) and Cephaloplectinae (Staphylinidae). Ann. Ent. Soc. Amer., 36: 546-586.

Séguy, E. 1946. Un nouveau Conopidae (Dipt.) du genre *Stylogaster* Macquart. Bull. Soc. Ent. Fr., 51: 99-100.

Sellnick, M. 1925. Die Gattung *Sphaeroseius* Berl. (Acar. Laelapt.). Ent. Mitt., 14: 5-11, pl. 1.

1926. Alguns novos Acaros (Uropodidae) myrmecophilos e termitophilos. Arch. Mus. Nac., Rio de Janeiro, 26: 29-56.

Seyfried, A. P. 1928. An anatomical-histological study of the myrmecophilous histerid *Chrysetaerius iheringi* Reichensperger. Contributions to Myrmecophily No. 2 (Thesis Univ. Fribourg, Switz.) 64 p.

Silvestri, F. 1932. Descrizione di un nuovo genere ecitofilo di Lepismidae (Insecta, Thysanura). Rev. Ent., Rio de Janeiro, 2: 133-138.

Smith, F. 1858. Catalogue of the Hymenopterous insects in the collection of the British Museum. Vol. VI. Formicidae. London: British Museum. 216 p., 14 pl.

Smith, M. R. 1942. The legionary ants of the United States belonging to *Eciton* subgenus *Neivamyrmex* Borgmeier. Amer. Midl. Nat., 27: 537-590, 7 pl.

Snyder, F. M. 1949. Revision of *Neomuscina* Townsend. Amer. Mus. Novit., no. 1404: 1-39.

1954. A revision of *Cyrtoneurina* Giglio-Tos, with notes on related genera (Diptera, Muscidae). Bull. Amer. Mus. Nat. Hist., 103: 417-464.

Standley, P. C. 1933. The flora of Barro Colorado Island, Panama. Contr. Arnold Arbor. Harvard Univ. No. 5: 1-178, pl. 1-21.

Sumichrast, F. 1868. Notes on the habits of certain Mexican Hymenoptera presented to the American Entomological Society. Trans. Amer. Ent. Soc., 2: 39-44.

Tafuri, J. F. 1955. Growth and polymorphism in the larva of the army ant (*Eciton* (*E*.) *hamatum* Fabricius). Jour. N. Y. Ent. Soc., 63: 21-41.

Thorpe, W. H. 1942. Observations on *Stomoxys* *ochrosoma* Speiser (Diptera Muscidae) as an associate of army ants (Dorylinae) in East Africa. Proc. R. Ent. Soc. London, (A)17: 38-41.

Townsend, C. H. T. 1897a. Contributions from the New Mexico Biological Station. - No. 2. On a collection of Diptera from the lowlands of the Rio Nautla, in the State of Vera Cruz. I. Ann. Mag. Nat. Hist., (6)19: 16-34.

1897b. Contributions from the New Mexico Biological Station. No. II. (continued). On a collection of Diptera from the lowlands of the Rio Nautla, in the State of Vera Cruz. II. Ann. Mag. Nat. Hist., (6)20: 19-33.

1912. Descriptions of new genera and species of muscoid flies from the Andean and Pacific coast regions of South America. Proc. U. S. Nat. Mus., 43: 301-367 (1913).

1914. Corrections to paper on Andean Muscoidea (Dipt.). Ent. News, 26: 28.

1916. New Neotropical muscoid flies. Proc. U. S. Nat. Mus., 49: 405-440 (1915).

1927. Synopse dos generos muscoideos de região humida tropical da America, com generos e especies novos. Rev. Mus. Paulista, 15: 205-369.

Villeneuve, J. 1922. Descriptions de six Tachinides nouveaux d'Afrique. Trans. Ent. Soc. London, 1921: 518-523.

Wasmann, E. 1896. Die Myrmecophilen und Termitophilen. Comptes Rendus 3me Congr. Internat. Zool., Leyde, p. 410-440 (1895).

1900. Neue Dorylinengäste aus dem neotropischen und dem äthiopischen Faunengebiet. Zool. Jb., Syst., 14: 215-289, pl. 13-14.

1904. Zur Kenntniss der Gäste der Treiberameisen und ihrer Wirthe am obern Congo, nach den Sammlungen und Beobachtungen von P, Herm. Kohl C. SS. C. bearbeitet. Zool. Jb., Suppl., 7: 611-682, pl. 31-33.

Weber, N. A. 1941. The rediscovery of the queen of *Eciton* (*Labidus*) *coecum* Latr. Amer. Midl. Nat., 26: 325-329.

1949. A new Panama Eciton (Hymenoptera, Formicidae). Amer. Mus. Novit., no. 1441: 1-8.

1956. Fungus-growing ants and their fungi: Trachymyrmex septentrionalis. Ecology, 37: 150-161.

1959. Isothermal conditions in tropical soil. Ecology, 40: 153-154.

Weld, L. H. 1960. A new genus of Cynipoidea (Hymenoptera). Proc. Ent. Soc. Wash., 62: 195-196.

Wheeler, G. C. 1943. The larvae of the army ants. Ann. Ent. Soc. Amer., 36: 319-332, 2 pl.

Wheeler, W. M. 1908. The ants of Texas, New Mexico and Arizona. Part I. Bull. Amer. Mus. Nat. Hist., 24: 399-485, 2 pl.

1910. Ants: their structure, development and behavior. New York: Columbia Univ. Press. xxv + 663 p.

1921. Observations on army ants in British Guiana. Proc. Amer. Acad. Arts Sci., 56: 289-328.

1928. The social insects, their origin and evolution. London: Kegan Paul, Trench, Trubner. xviii + 378 p.

1932. An extraordinary ant-guest from the Philippines (Aenictoteras chapmani, gen. et sp. nov.). Soc. Ent. Fr., Livre du Centenaire, p. 301-310.

Wheeler, W. M., and W. H. Long. 1901. The males of some Texan Ecitons. Amer. Nat., 35: 157-173.

Williams, E. C. 1941. An ecological study of the floor fauna of the Panama rain forest. Bull. Chicago Acad. Sci., 6: 63-124.

Williston, S. W. 1885. North American Conopidae: Conclusion. Trans. Connecticut Acad. Arts Sci., 6: 377-394, 1 pl.

Wilson, E. O. 1958. The beginnings of nomadic and group-predatory behavior in the ponerine ants. Evolution, 12: 24-31.

Wilson, E. O., T. Eisner and B. D. Valentine. 1954. The beetle genus *Paralimulodes* Bruch in North America, with notes on morphology and behavior (Coleoptera: Limulodidae). Psyche, Camb., Mass., 61: 154-161.

Woodring, W. P. 1958. Geology of Barro Colorado Island, Canal Zone. Smithson. Misc. Coll., 135(3): 1-39.

Woolf, B. 1957. The log likelihood ratio test (the G-test). Methods and tables for tests of heterogeneity in contingency tables. Ann. Hum. Genet., London, 21: 397-409.

Wulp, F. M. van der. 1888-1903. Biologia Centrali-Americana. Insecta. Diptera. vol. 2: x + 489 p., 13 pl.

Wygodzinsky, P. 1943. Nota sôbre um gênero de Lepismatídeo ecitófilo (Thysanura, Lepismatidae). Rev. Ent., Rio de Janeiro, 14: 260-262.

1958. Sobre algunos Nicoletiidae americanos (Thysanura, Insecta). Acta Zool. Lilloana, 16: 97-120.

VI. APPENDIX

List of Colonies of Army Ants Studied

The following list gives the colony number, species, and dates when the colony was observed in the field and laboratory. Colony designations for colonies observed before June 1955 are the same as those used by Dr. Schneirla. Information on the brood and a few of the more important observations are also included. More details are given for the species on which there has been little information published. All the colonies were studied by Carl W. and Marian E. Rettenmeyer on Barro Colorado Island unless other data is given.

In order to save space the following symbols are used: RC = raid column(s), RS = raid swarm, EC = emigration column, BTC = backtracking column, N-1 = first nomadic day or first day in the nomadic phase, S-1 = first statary day, N-last = last nomadic day, and S-last = last statary day. Question marks after nomadic or statary days indicate that these figures are estimates and the true position in the phase may differ by one to three days either side of the estimates. The methods used to measure the larvae and to determine the approximate position in the nomadic or statary phase are discussed in the section entitled Determining Ages of Broods and Position of Colony in Activity Cycle. The range of size or age of the brood is followed by the mean length of the ten smallest larvae or prepupae seen in the sample and the mean length of the ten largest larvae or prepupae seen in the sample. Since these larvae and prepupae were picked out by eye, somewhat greater variation undoubtedly existed within the broods. Although more brood samples were taken, only representative ones were measured.

E-101, *Neivamyrmex nigrescens* (Cresson), KANSAS: 5 miles northeast of Lawrence, University of Kansas Natural History Reservation, (C. W. Rettenmeyer and W. E. LaBerge), 28 June, S-1?, to 2 July 1955, bivouac; 30 June, somewhat physogastric queen taken, worker brood was rapidly metamorphosing to pupae; 10 July, S-13?, first callows emerged in laboratory; 12 July, remaining ants and brood preserved.

E-102, *Nomamyrmex esenbecki crassicornis* (F. Smith), 12 Feb. 1956, 9:45 to 11:40 a.m., 8:00 p.m., RC; 13 Feb., 10:15 a.m., RC.

E-103, *Eciton mexicanum panamense* Borgmeier, 12 Feb. 1956, 7:40 to 8:50 p.m., RC.

E-104, *E. hamatum* (Fabricius), 13 Feb. 1956, RC.

E-105, *E. hamatum*, [= E-104?], 13 Feb. 1956, N-3?, range of male larvae 5.2 to 10.8 mm., means 5.7 and 9.1 mm., mean of 57 larvae 7.4 mm.; 15 Feb., last observations.

E-106, *Noma. esenbecki crassicornis*, [= E-102?], 13 Feb. 1956, 6:20 p.m., RC.

E-107, *E. burchelli foreli* Mayr, 14 to 24 Feb. 1956; 20 Feb., N-9?, range of worker larvae 4.4 to 9.2 mm., means 5.3 and 8.2 mm.; 21 Feb., no EC; 22 Feb., EC about 110 meters; 23 Feb., larvae spinning, EC; 24 Feb., S-1.

E-108, *E. mexicanum panamense*, 14 Feb. 1956, 9:10 to 11:35 p.m., RC and EC, queen taken, three one-half to two-thirds grown larvae taken, 4.0, 4.8, and 6.0 mm.; 13 Feb., 11:20 a.m., BTC mostly under leaves.

E-109, *E. burchelli foreli*, 15 Feb. 1956, 6:00 to 6:40 p.m., RC with no swarms at front.

E-110, *E. burchelli foreli*, [= E-109?], 15 Feb. to 8 Mar. 1956, statary bivouac up tree; 5 Mar., N-1; 8 Mar., N-4, range of brood, eggs 0.4 mm. to larvae 2.4 mm., mean of ten largest larvae, 2.1 mm.

E-111 = E-107.

E-112, *E. dulcius crassinode* Borgmeier, 17 Feb. 1956, 11:20 to 11:30 p.m., RC.

E-113, *E. mexicanum panamense*, 20 Feb. 1956, 8:20 to 9:00 p.m., RC.

E-114, *E. hamatum*, 22 to 23 Feb. 1956.

E-115, *E. dulcius crassinode*, 23 Feb. 1956, 10:40 to 10:45 p.m., RC.

E-116, *Noma. esenbecki crassicornis*, 24 Feb. 1956, about 8:00 p.m., RC.

E-117, *E. dulcius crassinode*, 24 Feb. 1956, about 10:00 p.m., RC.

E-118, *Eciton* sp. probably *mexicanum*, 26 Feb. 1956, RC disappeared before sample could be taken.

E-119, *Labidus praedator sedulus* Menozzi, 26 Feb. 1956, 4:50 to 5:00 p.m., 6:00 to 6:10 p.m., RC disappeared at 6:10 p.m.

E-120, *L. praedator sedulus*, 27 Feb. 1956, 12:25 to 2:15 p.m., RC. RS stopped about 1:45 p.m.

E-121, *E. hamatum*, 27 Feb. to 22 Mar. 1956; 28 Feb. statary bivouac; 29 Feb. cocoon sample taken, all prepupae, range 4.0 to 11.2 mm., means 4.6 and 9.9 mm., physogastric queen taken, returned her to colony about five hours later; 17 Mar., S-last, S-19?; 18 Mar., N-1.

E-122, *Noma. esenbecki crassicornis*, 28 Feb. 1956, 8:45 to 9:10 a.m., RC.

E-123, *E. hamatum*, 2 Mar. 1956, RC.

E-124, *E. vagans mutatum* Borgmeier, 2 Mar. 1956, 11:20 to 11:40 p.m., RC.

E-125, *E. mexicanum panamense*, 3 Mar. 1956, 8:00 p.m., RC.

E-126, *L. praedator sedulus*, 4 Mar. 1956, 8:00 to 10:00 p.m., RS and RC.

E-127, *E. hamatum*, 5 to 8 Mar. 1956; 8 Mar., N-11?, range of worker larvae 2.0 to 8.4 mm., means 2.4 and 7.2 mm.

E-128, *E. mexicanum panamense*, 7 Mar. 1956, 9:45 to 10:00 p.m., RC.

E-129, *E. vagans mutatum*, 8 Mar. 1956, 11:30 to 11:40 a.m., 7:05 p.m., RC.

E-130, *L. praedator sedulus*, 8 Mar. 1956, 7:30 p.m., RS.

E-131, *L. praedator sedulus*, 15 Mar. 1956, 1:00 to 2:30 p.m., RS, RC.

E-132, *E. burchelli foreli*, 16 to 26 Mar. 1956, RC; 17 Mar., N-1; 19 Mar., N-3, still opening cocoons, no EC; 21 Mar., N-5, no EC.

E-133, *L. praedator sedulus*, 27 Mar. 1956, 10:50 to 11:15 a.m., RS, RC.

E-134, *E. hamatum*, 27 Mar. 1956, RC.

E-135, *E. mexicanum panamense*, 27 Mar. 1956, 7:00 to 7:20 p.m., 8:10 to 8:40 p.m., RC.

E-136, *E. burchelli foreli*, [= E-132?], 27 Mar. to 28 Apr. 1956; 31 Mar., larvae spinning, no EC; 2 Apr., range of worker brood, larvae 4.0 to prepupae 12.0 mm., means 4.4 and 10.6 mm., EC; 3 Apr., S-1, statary period 20 days; 23 Apr., N-1; 24 Apr., N-2, range of brood, eggs 0.4 mm. to larvae, 1.2 mm., means of largest larvae 1.2 mm.

E-137, *E. dulcius crassinode*, 2 Apr. 1956, 8:15 to 10:40 p.m., EC with callow workers, eggs and young larvae.

E-138, *L. praedator sedulus*, 6 Apr. 1956, 10:55 to 11:05 a.m., RS.

E-139, *E. hamatum*, 6 Apr. 1956, RC.

E-140, *E. burchelli* foreli, 7 Apr. 1956, RC.

E-141, *E. hamatum*, 8 Apr. 1956, N-2?, range of worker brood, eggs 0.4 mm. to largest larva 2.0 mm., mean of ten largest larvae 1.9 mm., queen taken from bivouac; 9 Apr., queen returned.

E-142, *E. burchelli foreli*, 11 Apr. 1956, RC.

E-143, *E. dulcius crassinode*, 11 Apr. 1956, 7:30 to 8:35 p.m., RC, EC.

E-144, *E. vagans mutatum*, 12 Apr. 1956, 9:30 to 10:00 p.m., RC.

E-145, *E. vagans mutatum*, [= E-144?], 13 Apr. 1956, 6:30, 10:00 p.m.; 15 Apr., 6:15, 10:30 p.m., RC.

E-146, *L. praedator sedulus*, 15 Apr. 1956, 9:00 to 10:00 p.m.; 16 Apr. 1:30 to 1:45 a.m., 4:30 to 5:00 a.m., 7:00 a.m., clusters outside bivouac (?) under foundation at northwest corner of old laboratory, no RC or EC found.

E-147, *E. mexicanum panamense*, 18 Apr. 1956, 7:40 to 10:00 p.m., RC; 19 Apr., 12:40 to 12:55 a.m., RC.

E-148, *E. burchelli foreli*, [= '52 B-IX by marked queen], 18 Apr. 1956, range of worker brood, full-grown larvae to prepupae in cocoons; 19 Apr., N-last, statary phase of 21 days; 11 May, N-1; 12 May, no EC; 13 May, N-3, no EC; 14 May, EC; 15 May, queen taken on EC; 16 May, queen returned, EC; 17 May, N-7, no EC; 18 May, EC; 19 May, EC; 20 May, N-10, queen taken from bivouac and preserved in Bouin's fixative, range of worker larvae 1.6 to 7.2 mm., means 1.8 to 4.1 mm.; 26 May, N-16, range 6.0 to 10.8 mm., means 6.8 and 9.8 mm.; 24 May to 28 May colony combined with E-156.

E-149, *E. burchelli foreli*, 19 Apr. 1956, 3:30 p.m., three alate males found in bivouac; 20 Apr., N-10?, range of worker larvae, 2.4 to 12.8 mm., means, 2.9 and 10.5 mm., EC not followed.

E-150, *Neivamyrmex* sp. or *Labidus praedator sedulus*, 21 Apr. 1956, 8:15 to 8:16 p.m., RC disappeared before sample could be taken.

E-151, *E. mexicanum panamense*, 25 Apr. 1956, 6:20 to 9:45 p.m., RC.

E-152, *E. burchelli foreli*, 28 Apr. 1956, EC.

E-153, *E. mexicanum panamense*, 28 Apr. 1956, 10:00 to 10:40 p.m., EC with many callows, no immature brood seen.

E-154, *E. vagans mutatum*, 29 Apr. 1956, S-1?, 6:30 to 8:15 p.m., RC, subterranean bivouac close to surface, range of 11 worker larvae, 7.6 to 12 mm., mean 10.0 mm.; 30 Apr. 8:00 to 8:45 a.m., dug out part of bivouac, worker pupae white; 6:30 p.m., few workers found at cavity; 9:15 p.m., RC; 22 May, S-24?, 8:00 a.m., first major workers emerged in laboratory from sample taken on 30 Apr.

E-155, *Noma. esenbecki crassicornis*, 29 Apr. 1956, 8:30 to 8:40 p.m., RC.

E-156, *E. burchelli foreli*, 30 Apr. 1956, N-last, range of larvae 3.2 to 12 mm., means 3.8 and 9.8 mm.; 1 May, S-1, statary phase 21 days; 22 May, N-1, EC; 23 May, EC; 24 May, EC; 25 May, N-4, no EC; 26 May, no EC, range of worker larvae 1.2 to 4.4 mm., means 1.7 mm. and 4.1 mm.; 27 May, no EC; 24 to 28 May colony E-148 fused with E-156; 28 to 30 May, EC each night; 31 May, N-10, no EC; 1 June, EC, range of worker larvae 2.4 to 4.0 mm., means 3.3 and 9.0 mm.

E-157, *E. mexicanum panamense*, 30 Apr. 1956, 6:45 to 9:00 p.m., RC.

E-158, *Neivamyrmex gibbatus* Borgmeier, 3 May 1956, 3:25 to 4:35, 5:50 to 5:55 a.m., RC.

E-159, *E. hamatum*, 11 May 1956, RC, EC, 8:05 p.m., queen taken; 12 May, 3:30 a.m., no BTC, 6:00 a.m., strong BTC to previous bivouac; 13 to 14 May, BTC; 14 May, 10:00 a.m., queen returned.

E-160, *Noma. esenbecki crassicornis*, 14 May 1956, 8:10 to 10:00 a.m., end of EC and brief RC.

E-161, *Neiv. pilosus mexicanus* (F. Smith), 14 May 1956, 10:00 to 10:10 a.m., RC.

E-162, *E. hamatum*, 15 May 1956, EC; 16 May, EC, range of worker brood, eggs 0.4 mm. to larvae 3.6 mm., means of largest larvae 3.2 mm.; 19 to 23 June, colony found again, identified by marked queen, E-170, 24 May 1956, *E. mexicanum panamense*, 24 May 1956, 6:20 to 10:20 p.m., EC, worker larvae about one-half grown, range of larvae 1.2 to 6.0 mm., means 1.6 and 5.3 mm.

E-171, *Noma. esenbecki crassicornis*, [= E-164?], 25 May 1956, 6:45 a.m., RC.

E-172, *E. burchelli foreli*, [= E-148], 25 May 1956, bivouac.

E-173, *E. hamatum*, 27 May 1956, RC.

E-174, *Neiv. pilosus mexicanus*, 28 May 1956, 1:25 to 1:45 p.m., RC.

E-175, *E. mexicanum panamense*, 29 May 1956, 12:40 to 12:50 a.m., 1:30 to 1:50 a.m., RC.

E-176, *Neiv. pilosus mexicanus*, 29 May 1956, 10:00 to 10:10 a.m., RC.

E-177, *L. praedator sedulus*, 29 May 1956, 7:10 to 7:30, 9:45 to 10:10 p.m., RC; 30 May, 6:45 to 11:00 a.m., EC.

E-178, *E. mexicanum panamense*, 30 May 1956, 7:25 to 7:40 p.m., RC.

E-179, *L. coecus*, 31 May 1956, 7:45 to 8:10 p.m., 10:45 to 10:50 p.m., RS.

E-180, *E. vagans mutatum*, 31 May 1956, 8:15 to 9:50 p.m., 10:15 to 10:30 p.m., EC, range of worker larvae 1.2 to 6.8 mm., means 1.8 and 5.8 mm., queen taken; 1 June, 9:00 p.m., 10:00 p.m., BTC.

E-181, *E. mexicanum panamense*, 1 June 1956, 10:15 to 10:30 p.m., RC.

E-182, *L. praedator sedulus*, 2 June 1956, 10:00 to 11:30 a.m., 6:00 to 6:30 p.m., RC; 4 June, 9:00 a.m., RC.

E-183, *L. praedator sedulus*, [= E-182?], 3 June 1956, 6:45 to 7:00, 8:00 to 8:30 a.m., 8:00 to 8:15 p.m., RC; 4 June, 2:45 to 4:00 a.m., 7:00 a.m., 7:55 to 10:40 a.m., RC or EC; 6:00, 9:30, and 11:00 p.m., RC; 5 June, 3:30 to 6:45 a.m., RC or EC, range of five larvae 3.2 to 4.0 mm.; 7:00, 8:30 p.m., RC.

E-184, *E. mexicanum panamense*, 4 June 1956, 2:45 to 2:50, 3:20 to 4:30 p.m., RC and bivouac.

E-185, *L. praedator sedulus*, [= E-177?], 5 June 1956, 2:30 to 2:35 a.m., RC.

E-186, *E. hamatum*, 6 June 1956, RC, statary bivouac, worker pupae white.

E-187, *E. mexicanum panamense*, 11 June 1956, 7:30 to 8:00 p.m., RC.

E-188, *E. mexicanum panamense*, [= E-187?], 13 June 1956, 10:40 to 10:45 p.m., RC.

E-189, *E. hamatum*, 16 June 1956, queen taken from bivouac, range of worker larvae 3.6 to 11.2 mm., means 4.3 and 9.2 mm., EC; 17 June, 6:45 to 7:20 p.m., RC, no EC.

E-190, *E. mexicanum panamense*, [= E-187?, E-188?], 17 June 1956, 9:30 p.m., RC.

E-191, *E. hamatum*, [= E-162 by marked queen].

E-192, *E. hamatum*, 22 June 1956, exceptionally large colony found with three RC, possibly colony E-168 and E-189 had combined with this colony, brood of worker larvae and prepupae in cocoons being carried to an exposed bivouac, one larva taken, 5.6 mm., range of largest prepupae 8.0 to 12.4 mm., mean 10.4 mm.

E-193, *L. coecus*, 22 June 1956, 10:00 to 10:15, 10:30 to 10:35 p.m., RS.

E-194, *E. dulcius crassinode*, 23 June 1956, 5:00 to 6:30 p.m., RC.

E-195, *E. mexicanum panamense*, 23 June 1956, 11:00 to 11:05 p.m., RC.

E-196, *E. hamatum*, 24 June 1956, RC.

E-197, *E. mexicanum panamense*, [= E-195?], 24 June 1956, 8:00 to 8:05, 9:20 to 9:30 p.m., RC.

E-198, *E. vagans mutatum*, 24 June 1956, 9:00 to 9:30 p.m., RC.

E-199, *Noma. esenbecki crassicornis*, 29 June 1956, 8:00 to 8:20 a.m., RC.

E-200, *E. hamatum*, 30 June 1956, RC, EC, bivouac.

E-201, *L. coecus*, 1 July 1956, midnight to 2:00 a.m., RS.

E-202, *L. praedator sedulus*, 1 July 1956, 4:45 to 4:50, RC.

E-203, *E. hamatum*, 2 July 1956, RC.

E-204, *E.dulcius crassinode*, 4 July 1956, 3:30 to 5:40 a.m., EC, 7:45 to 8:30 a.m., dug out part of bivouac, range of worker larvae 2.0 to 8.4 mm., means 4.1 and 7.3 mm., 5:00 p.m., RC or BTC, 7:15 to 7:56 p.m., EC, 8:00 to 9:00 p.m., RC; 5 July, 4:00 to 4:30 a.m., RC, BTC, 8:00 to 9:00 p.m., worker larvae almost full grown, range of larvae 2.8 to 11.6 mm., means 3.7 and 9.6 mm., EC; 6 July, 8:00 to 10:00 p.m., BTC; 9 July, about 8:00 p.m., BTC; 10 July, 1:00, 6:00 a.m., BTC.

E-205, *L. coecus*, 4 July 1956, 8:10 to 8:15 p.m., RC.

E-206, *E. hamatum*, 5 July 1956, RC.

E-207, *L. praedator sedulus*, 5 July 1956, 10:30 to 11:00 a.m., RS.

E-208, *Noma. esenbecki crassicornis*, 5 July 1956, 11:20 a.m., RC.

E-209, *E. vagans mutatum*, 5 July 1956, about 11:50 a.m., RC.

E-210, *Noma. esenbecki crassicornis*, 7 July 1956, 8:45 to 9:25 a.m., RC.

E-211, *E. hamatum*, 7 July 1956, N-8?, RC, bivouac, range of worker larvae 0.8 to 4.8 mm., means 1.0 and 4.1 mm.; 9 July, range of worker larvae, 0.8 to 6.0 mm., means 1.5 and 5.3 mm.

E-212, *E. vagans mutatum*, 9 July 1956, 10:50 to 11:45 a.m., RC, bivouac, range of male larvae 16.0 to 17.6 mm., means 16.6 and 17.4 mm.

E-213, *L. coecus*, 10 July 1956, 1:00 to 8:00 a.m., RS watched intermittently.

E-214, *E. vagans mutatum*, PANAMA: Canal Zone: Mt. Hope Railroad Station, 17 July 1956, 7:00 a.m., RC.

E-215, *Noma. esenbecki crassicornis*, 18 July 1956, 11:25 to 11:30 a.m., end of RC or EC.

E-216, *L. praedator sedulus*, 18 July 1956, 8:40 to 9:25, 9:40 to 10:10 p.m., RS.

E-217, *L. praedator sedulus*, 21 July 1956, 12:15 to 1:00 p.m., RS.

E-218, *Neiv. pilosus mexicanus*, 22 July 1956, 11:35 to 11:55 a.m., RC.

E-219, *E. vagans mutatum*, 24 July 1956, N-2?, 2:30 to 4:00 a.m., range of worker brood, eggs 0.4 mm., larvae 0.4 to 3.2 mm., mean of largest larvae 2.6 mm., EC, 6:00, 9:00 to 10:00 p.m., BTC; 25 July, 7:00 a.m., BTC, BTC seen several times during night; 26 July, 7:00 to 8:00 a.m. BTC decreased, about 4:00 p.m. BTC resumed, 8:30 p.m. queen returned to BTC.

E-220, *L. praedator sedulus*, 25 July 1956, 10:00 a.m. to 1:00 p.m., RS.

E-221, *E. hamatum*, 26 July 1956, N-6?, RC, bivouac, EC, range of worker larvae 1.6 to 4.8 mm., means 2.0 and 4.4 mm.

E-222, *E. burchelli foreli*, 26 July 1956, N-9?, range of worker larvae 5.2 to 10.8 mm., means 5.6 and 8.4 mm., RS, bivouac, EC; 29 July, BTC, queen returned.

E-223, *E. mexicanum panamense*, 26 July 1956, 6:10 to 6:15 p.m., RC.

E-224, *Neiv. humilis* (Borgmeier), 26 July 1956, 11:00 to 11:30 p.m., RC.

E-225, *L. praedator sedulus*, 27 July 1956, 9:55 to 10:20 a.m., RS, 10:20 to 11:15 a.m., RC.

E-226, *E. hamatum*, [= E-221?], 29 July 1956, S-2?, range of prepupal worker brood 4.4 to 9.6 mm., means 4.5 and 8.9 mm., pupae with short leg buds and white with expanded legs; 5 Aug., S-9?, brood of eggs, brood of white pupae.

E-227, *Neiv. pilosus mexicanus*, 29 July 1956, 9:50 to 10:50 a.m., RC, range of larvae 2.4 to 4.8 mm., means 2.7 and 4.2 mm.

E-228, *L. coecus*, 29 July 1956, 9:30 to 9:45 p.m., RC.

E-229, *E. burchelli foreli*, 30 July 1956, N-8?, range of worker larvae 1.2 to 10.0 mm., means 1.5 and 8.6 mm.

E-230, *L. praedator sedulus*, 31 July 1956, 9:55 to 11:20 a.m., RS, 11:20 a.m. to 12:40 p.m., RC.

E-231, *L. praedator sedulus*, 1 Aug. 1956, 12:40 to 1:40 p.m., RS.

E-232, *E. hamatum*, 4 Aug. 1956, RC.

E-233, *E. hamatum*, 5 Aug. 1956, RC, bivouac.

E-234, *Neiv. pilosus mexicanus*, 5 Aug. 1956, 10:00 to 10:20 a.m., RC.

E-235, *E. vagans mutatum*, 5 Aug. 1956, 11:00 to 11:15 a.m., RC.

E-236, *L. praedator sedulus*, 7 Aug. 1956, 9:00 to 9:10 a.m., RS.

E-237, *E. hamatum*, 7 Aug. 1956, RC.

E-238, *E. burchelli foreli*, 7 Aug. 1956, N-5?, RS, bivouac, range of worker brood, eggs 0.4 mm. to larvae 7.2 mm., mean of ten largest larvae 6.0 mm., EC; 8 Aug., EC; 9 Aug., N-7?, range of worker brood, eggs 0.4 mm. to larvae 8.4 mm., mean of ten largest larvae 6.6 mm., EC; 10 Aug., range of worker larvae 3.6 to 10.0 mm., means 4.1 and 9.1 mm., EC; 11 Aug., N-9?, 10:45 a.m., completing move to second bivouac about 20 meters beyond one started night of 10 Aug., range of larvae 4.4 to 11.6 mm., means 5.0 and 9.9 mm., EC, colony lost.

E-239, *E. mexicanum panamense*, 7 Aug. 1956, 7:45 to 7:50 p.m., 11:05 to 11:15 p.m., EC with many callows but no eggs or larvae seen.

E-240, *E. vagans mutatum*, 7 Aug. 1956, N-3?, 8:15 to 9:20, 10:00 to 10:50, 11:10 p.m., EG with alate males, two eggs and two larvae

0.8 mm. long also taken; 8 Aug., 7:05 to 7:10, 8:30 to 8:40 p.m., RC; 9 Aug., 7:30, 8:05 p.m., RC.

E-241, Neiv. gibbatus, 7 Aug. 1956, 9:25 to 9:30, 9:45 to 9:50 p.m., RC; 8 Aug., 7:15 to 7:25 p.m., RC.

E-242, E. dulcius crassinode, 7 Aug. 1956, 9:25 to 9:45 p.m., RC.

E-243, E. hamatum, 8 Aug. 1956, EC, queen taken, worker larvae about three-fourths grown, range of larvae 2.4 to 8.8 mm., means 2.6 and 7.8 mm.; 9 Aug., 7:30 to 8:00 p.m., BTC, bivouac, range of worker larvae 3.6 to 10.4 mm., means 4.4 and 9.0 mm.

E-244, E. mexicanum panamense, 8 Aug. 1956, 8:15 to 8:20 p.m., RC.

E-245, E. hamatum, 9 Aug. 1956, RC.

E-246, E. hamatum, 11 Aug. 1956, N-13?, RC; 12 Aug., range of worker larvae 2.4 to 9.2 mm., means 2.5 and 8.3 mm.

E-247, E. hamatum, 12 Aug. 1956, RC.

E-248, E. burchelli foreli, 12 Aug. 1956, RC, bivouac, range of worker larvae 4.4 to 12.0 mm., means 3.2 and 10.6 mm.; EC.

E-249, E. burchelli foreli, 12 Aug. 1956, N-10?, RC, bivouac, range of worker larvae, 3.6 to 12.8 mm., means 3.9 and 10.0 mm., EC.

E-250, E. hamatum, 12 Aug. 1956, EC, bivouac.

E-251, E. mexicanum panamense, 12 Aug. 1956, 8:30 to 8:35, 9:10 to 9:15 p.m., worker larvae about three-fourths grown, range of larvae 1.2 to 8.0 mm., means 1.2 and 7.2 mm.

E-252, E. mexicanum panamense, 12 Aug. 1956, 10:00 p.m., RC.

E-253, E. burchelli foreli, 16 Aug. 1956, N-11?, range of worker larvae 3.6 to 12.4 mm., means 4.4 and 10.2 mm., EC; 17 Aug., N-12?, range of larvae 4.4 to 13.2 mm., means 5.2 and 11.6 mm., EC.

E-254, E. mexicanum panamense, 16 Aug. 1956, 9:00 p.m., RC.

E-255, *E. mexicanum panamense*, 16 Aug. 1956, 11:45 p.m., RC.

E-256, *E. mexicanum panamense*, 17 Aug. 1956, 9:15 to 9:20 p.m., worker larvae about two-thirds grown, range of larvae 3.6 to 7.6 mm., means 4.5 and 7.0 mm.

E-257, *E. mexicanum panamense*, 17 Aug. 1956, 10:00 to 10:15 p.m., RC.

E-258, *E. hamatum*, 19 Aug. 1956, RC.

E-259, *Neiv. pilosus mexicanus*, 6 June 1956, 5:30 to 7:00 a.m., RC.

E-260, *Neiv. opacithorax* (Emery), KANSAS: University of Kansas Natural History Reservation, 10 Apr. 1957, 5:00 p.m., 6:00 p.m., cluster under rock.

E-261, *Neiv. nigrescens* (Cresson), same locality as E-260, 4 May 1957, 6:30 to 7:30 p.m., cluster under rock.

E-262, *Neiv. opacithorax* (Emery), KANSAS: 1 mile west of Lawrence, 18 May 1957, 2:00, 4:00 p.m., cluster under rock.

E-263, *Neiv. opacithorax*, KANSAS: 1 mile northwest of Lawrence, 26 May to 2 June 1958, statary colony with RC daily; 3 June, 7:40 to 8:30 a.m., RC; 10:25 p.m. to 4 June, 1:31 a.m., EC, physogastric queen taken; 4 June, 6:20 to 6:40 p.m., two workers seen wandering near holes, 10:15 to 10:45 p.m., BTC; 5 June, 2:30 p.m., BTC, 9:45 to 9:50 p.m., BTC.

E-264, *Neiv. opacithorax*, KANSAS: Lawrence, on campus of University of Kansas, crossing sidewalk west of Snow Hall, 6 July 1959, 11:30 to 11:40 a.m., 12:40 p.m., RC, 7:15 p.m. to 7 July 1:35 a.m., RC and EC; 7 July, 10:00 a.m. to 10 July, 10:00 a.m., BTC apparently continuous; 10 July, 6:00 p.m., no BTC; 11 July, several times during day saw no BTC.

E-265, Neiv. nigrescens, KANSAS: 5 mi. northeast of Lawrence, University of Kansas Natural History Reservation, 21 July 1959, 6:00 p.m. to 10:06 p.m., RC; 22 July, 6:00 to 8:00 p.m., RC.

E-266, Neiv. opacithorax, KANSAS: Lawrence, in city between Tenth and Eleventh Streets along Ohio Street, 19 Aug. 1959, 9:00 p.m. to 20 July, 3:20 a.m., EC; 20 Aug., 7:30 to 7:40 p.m., RC or BTC.

E-267, Neiv. opacithorax, KANSAS: 1 mile east of Lawrence, 21 Oct. 1959, bivouac under house, alate males and workers coming into house through crack in floor about 2:00 p.m.; 22 Oct. clusters found on opposite sides of house.

'52 P-7, L. praedator sedulus, Barro Colorado Is. (T. C. Schneirla and C. W. Rettenmeyer) 19 Mar. 1952, 10:20 a.m. to 2:20 p.m., bivouac in rotten log and soil beneath log, took one dealate and 146 alate males, eggs, worker larvae of all ages, and cocoons with larvae, prepupae and white pupae.

'55 B-IV, E. burchelli foreli, Barro Colorado Is. (T. C. Schneirla and C. W. Rettenmeyer) 9 Feb. to 11 Feb. 1955 end of nomadic phase with sexual larvae; 12 Feb., S-1; 3 Mar., S-21; 4 Mar., N-1, colony divided into colonies '55 B-IV-N and B-IV-S: 16 Mar., N-13, collected large sample of adults and brood of worker larvae of B-IV-S; queen killed?; 17 Mar., N-14, took queen on EC at 12:10 a.m., collected most of brood and large sample of B-IV-N at 12:30 p.m.. BTC between two colonies observed several times up to 24 Mar.

Table 1. Observations of Queens of Army Ants

Along Emigration Columns

Species	Date	Queen	Time	Distance in meters from old bivouac
Eciton hamatum	2 Mar. 1956	E-123	9:55 p.m.	?
	6 Mar. 1956	E-127	7:36 p.m.	10
	8 Mar. 1956	E-127	before 6:00 p.m.	0
	18 Mar. 1956	E-121	8:00 p.m.	5
	19 Mar. 1955	'55 H-E	10:06 p.m.	68
	28 Mar. 1955	'55 H-I	11:15 p.m.	15
	8 Apr. 1956	E-141	7:00 p.m.	7
	11 Apr. 1956	E-141	6:31 p.m.	6
	11 May 1956	E-159	8:05 p.m.	30
	15 May 1956	E-162	8:40 p.m.	>25
	16 May 1956	E-162	7:15 p.m.	10
	13 June 1956	E-168	7:15 p.m.	10
	23 June 1956	E-191	7:11 p.m.	5
	8 Aug. 1956	E-243	10:37 p.m.	>25
Eciton burchelli	17 Feb. 1956	E-107	8:25 p.m.	8
	23 Feb. 1956	E-107	10:15 p.m.	2
	5 Mar. 1956	E-110	11:15 p.m.	>20
	7 Mar. 1956	E-110	9:10 p.m.	100
	16 Mar. 1955	'55 B-IV-N	11:03 p.m.	90

Table 1 (continued). Observations of Queens of Army Ants Along Emigration Columns

Species	Date	Queen	Time	Distance in meters from old bivouac
Eciton burchelli (continued)	17 Mar. 1956	E-132	9:25 p.m.	20
	23 Mar. 1956	E-132	8:15 p.m.	22
	30 Mar. 1956	E-136	8:37 p.m.	60
	2 Apr. 1956	E-136	7:45 p.m.	25
	28 Apr. 1956	E-136	9:10 p.m.	10
	15 May 1956	E-148	8:05 p.m.	1
	26 July 1956	E-222	9:30 p.m.	20
Eciton vagans	30 May 1956	E-180	8:50 p.m.	>15
	24 July 1956	E-219	3:03 a.m.	>10
Eciton dulcius	1 Mar. 1955	'55 D-1 Mar.	9:00 p.m.	>30
	2 Apr. 1956	E-137	8:30 p.m.	>4
	11 Apr. 1956	E-143	8:30 p.m.	>10
	4 July 1956	E-204	7:41 p.m.	>20
Eciton mexicanum	14 Feb. 1956	E-108	9:40 p.m.	>8
	24 May 1956	E-170	10:15 p.m.	>5
	12 Aug. 1956	E-251	9:15 p.m.	>5
Nomamyrmex esenbecki	18 May 1956	E-164	10:28 p.m.	>3
Neivamyrmex opacithorax	3 June 1958	E-263	12:06 a.m.	1?
	6 July 1959	E-264	11:41 p.m.	>2

Table 2. Relative Attraction of Workers to Parts of Queens

Species	Queen No.	Alitrunk	Petiole	Segments of Gaster				
				1st	2nd	3rd	4th	5th
Eciton hamatum	E-123	x	x	27	16	11	1	0
E. dulcius crassinode	E-143	x	6	18	12	4	7	4
Eciton mexicanum	E-170	6	3	0	3	4	2	1
Nomamyrmex esenbecki	E-164	1	5	8	21	25	29	28

x = no record made but little attraction to this part of queen; for further explanation see text.

Table 3. Workers of Ecitonini Examined from Barro Colorado Island

Species of Ant	Workers other than Majors	Majors	All Workers	Larvae	Colonies	Samples	Samples 51+	Samples 101+
E. burchelli foreli	494,873	2,605	497,478	98,074	18	54	46	38
E. hamatum	32,517	2,207	34,724	29,939	30	52	32	28
E. dulcius crassinode	4,687	109	4,796	1,261	11	22	9	5
E. vagans ~~*angustatum*~~ mutatum	13,236	343	13,579	187	13	27	12	8
E. mexicanum panamensis	4,331	245	4,576	602	29	35	7	5
L. praedator sedulus	24,397	----	24,397	193	22	32	22	15
L. coecus	10,727	----	10,727	0	7	9	9	6
Noma. esenbecki crassicornis	3,481	----	3,481	94	14	25	10	5
Neiv. gibbatus	1,736	----	1,736	0	2	2	2	2
Neiv. humilis	622	----	622	0	1	1	1	1
Neiv. pilosus mexicanus	3,080	----	3,080	120	8	10	8	7
Neiv. postcarinatus	282	----	282	0	1	1	1	1
Neiv. pseudops	231	----	231	0	1	1	1	1
Total	594,200	5,509	599,709	130,470	157	271	160	127

Table 4. Workers of Ecitonini Examined from Other Localities

Species of Ant	Workers other than Majors	Majors	All Workers	Larvae	Colonies	Samples	Samples 51+	Samples 101+
E. burchelli parvispinum	21	0	21	0	1	1	0	0
E. burchelli foreli	6,020	122	6,142	0	3	3	1	1
E. burchelli urichi	7,338	25	7,363	341	15	15	4	2
E. burchelli cupiens	6,501	101	6,602	0	2	2	1	1
E. hamatum	10,072	213	10,285	10,000	4	4	1	1
E. lucanoides conquistador	120	0	120	0	3	3	0	0
E. vagans angustatum	2,000	1	2,001	0	2	2	1	1
L. praedator	559	----	559	50	4	4	1	1
L. coecus	617	----	617	500	5	5	3	2
Noma. esenbecki	50	----	50	0	4	4	0	0
Noma. hartigi	642	----	642	0	2	2	2	1
Neiv. legionis	250	----	250	0	1	1	1	1
Neiv. nigrescens	14,232	----	14,232	74	5	14	10	8
Neiv. opacithorax	1,137	----	1,137	0	6	6	4	3
Neiv. pilosus	208	----	208	0	4	4	1	0
Neiv. sumichrasti	86	----	86	0	2	2	0	0
Total	49,853	462	50,315	10,965	63	72	30	22

Table Summary of *Stylogaster* Collection Records

Taken near ant species:	Species of *Stylogaster*													Totals			
	banksi			*currani*			*minuta*			*panamensis*	*speciosa*		*stylosa*				
	♂	♀	?	♂	♀	?	♂	♀	?	♀	♀	?	♂	♂	♀	?	T
L. praedator	4	7	1	1	3	-	7	4	-	-	5	-	-	12	19	1	32
E. burchelli	9	8	1	6	8	1	3	9	4	2	1	1	1	19	28	7	54
E. hamatum	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	2
E. vagans	-	-	-	1	-	-	1	-	1	-	-	-	-	2	-	1	3
Not near ants	-	-	-	1	1	-	-	-	-	-	-	-	-	1	1	-	2
Totals	13	15	2	9	12	1	11	15	5	2	6	1	1	34	50	9	93
Both sexes	30			22			31			2	7		1				93

Table Stylogaster Eggs Found on Tachinidae

Field No.	Species of *Stylogaster*	Species of Tachinidae	Location of Egg on Tachinid
2341-A	*banksi*	*C. dives* ♀	Lateral, between terga II and III
1755-A	*currani*	*C. agilis* ♀	Lateral, between terga II and III
2329-A	*currani*	*C. agilis* ♀	Lateral, between terga I and II (see fig. 61)
2329-B	*currani*	*C. agilis* ♀	Ventral, between terga I and II
2341-B	*currani*	*C. agilis* ♀	Ventral, between terga II and III
2242-J	*currani*	*C. dives* ♀	Thorax, slightly anterodorsal of wing base
2341-C	*currani*	*C. venteris* ♀	On wing near base, first instar larva in egg, (see figs. 75-77)
2201-A	*currani*	*C. interrupta* ♀	Dorsum of ovipositor
1171-A	*minuta*	*A. ecitonis* ♀	Dorsolateral, between terga II and III
1446-C	*minuta*	*C. agilis* ♀	Ventrolateral part of eye (see fig. 62)
1854-A	*minuta*	*C. agilis* ♀	Dorsolateral part of eye
2257-F	*minuta*	*C. fumosa* ♀	Dorsal, between terga I and II
1446-G	*minuta*	*C. panamensis* ♀	Dorsolateral part of eye
1411-A	*speciosa*	*A. ecitonis* ♂	Pteropleuron, just below base of wing
1172-A	sp. a	*C. agilis* ♀	Lateral, between terga II and III
1446-F	sp. a	*C. dives* ♀	Lateral, between terga III and IV
1277-B	sp. a	*C. interrupta* ♀	Lateral, between terga II and III

Table 7. Summary of Collection Records for Tachinidae

Species of *Calodexia* or *Androeuryops*	Number and % over *Eciton burchelli* swarm raids		Number and % over *Labidus praedator* swarm raids		Total over both species	G-test
C. agilis	194	69%	87	31%	281	0.21 n. s.
C. apicalis	0	0	2	100	2	------
C. bella	50	91	5	9	55	13.85***
C. continua	85	71	34	29	119	0.07 n. s.
C. dives	60	30	137	70	197	132.89***
C. fasciata	190	78	53	22	243	7.65***
C. fumosa	24	28	61	72	85	63.92***
C. interrupta	105	65	56	35	161	1.95 n. s.
C. major	29	64	16	36	45	0.72 n. s.
C. panamensis	2	7	27	93	29	52.45***
C. similis	77	73	28	27	105	0.46 n. s.
C. varia	4	44	5	56	9	2.60 n. s.
C. venteris	345	79	89	21	434	18.79***
Calodexia total	1165	66	600	34	1765	14.77***
A. ecitonis	483	91	46	9	529	138.82***

*** $P = < 0.001$ n. s. = not significant

Table . Diagnostic Characters For Known Species Of Calodexia

Characters
1. Color of occipital pollen: white to yellowish (w); black (b).
2. Downward extent of black occipital bristles: 1/2; 2/3; 3/4; 4/4.
3. Width of palp: about equal (e); greatly enlarged near apex (en).
4. Color of third antennal segment distal to the insertion of the arista.
5. Number of pairs of presutural acrosticals.
6. Number of pairs of postsutural acrosticals.
7. Anterior extent of outer dark vittae compared with median sublaterals.
8. Median dark vittae behind suture: united; separated by light pollen.
9. Outer postsutural light vittae: absent (a); narrow (n); equal (e).
10. Dorsum of scutellum: white; black; white with basal black band (bb).
11. Number of pairs of lateral marginal scutellar bristles.
12. Color of pile on sternopleura and lower anterior mesopleura.
13. Notopleural hair: absent (a); color when present (b, w, y).
14. Infrasquamal cilia: black or occasionally absent (b); yellow (y).
15. Color of anterior surface of front coxae (ignoring pollen).
16. Color of hairs on front coxae (not including bristles).
17. Total number of black hairs and bristles on one front coxa.
18. Number of ventral bristles near middle of middle tibia.
19. Number of anterior bristles near middle of middle femur.
20. Ventral color of posterior femora: proximally orange (po); entire color.
21. Number of rows of ventral yellow cilia on posterior femur.
22. Color of dorsal abdominal pollen.

Table (continued)

	Characters
23.	Color of dorsum of first tergum and stripe (s) if present.
24.	Dorsal white pollen on first tergum: dense (dwp); absent or weak (a).
25.	Ventral pollen on first tergum: absent; equal to second; absent on both.
26.	Pollen on second tergum: interrupted by narrow or wide stripe or none.
27.	Median marginals on second tergum: number of pairs; or a row.
28.	Number of pairs of lateral and ventral marginals on second tergum.
29.	Pollen of third tergum: extended; not extended to median margin.
30.	Number of discals on third tergum.
31.	Color of central area of fourth tergum (ignoring pollen).
32.	Dark fascia on fourth tergum extending basad: 1/2; 2/3; 3/4; 4/4; absent.
33.	Discals on fourth tergum: number; or row of unknown number.
34.	Minimum body length in millimeters of length of single specimen.
35.	Maximum body length in millimeters.
36.	Number of specimens examined.

Table (continued)

Characters	*continua*	*interrupta*		*dives*	*caudata*	*similis*		*agilis*	*varia*	*mexicana*
	♀	♀	♂	♀	♂	♀	♂	♀	♀	♀
1.	w	w	w	w	w	w	w	w	w	w
2.	1-*2*	2	2	2	2-3?	1-2	3	2-*3*	4	?
3.	e	e	e	e	e?	e	en	e	e	?
4.	o-obr	o-obr	o-obr	o-br	o?	o-br	br-b	*o*-obr	o-*br*	br
5.	1	1	1	0	1	*1*-2	1	1	1	2
6.	1	1	1	1	1	*1*-2	1	1	3	3
7.	ea	ea	ea	ea	?	ea	ea	ea	ea	?
8.	u	u	u	u	u	u	u	u	sel	?
9.	n	n-*e*	n-*e*	n	n-e?	n	n	n-e	n	?
10.	bb	bb	bb	bb	bb?	bb	bb	bb	w	bb?
11.	3	3	3	2-*3*	3	3	3	*3*-4	3	3
12.	w	w-*y*	w-*y*	w	w	w	w	b	b	?
13.	w	a-*b*	b	b	w	w-y-*b*	w-y	b	b	?
14.	b	b	b	b	b	b	b	b	b	?
15.	o-br	o-*br*	o-br	o-br	o-br?	o-br	o-br	o-obr	o-*br*	?
16.	w	*b* + w	*b* + w	w	w, b?	w	w	b	b	?
17.	10-18	20-50	20-50	9-15	?	5-10	25-35	40-55	50+	?
18.	1-*2*	1	1	1	1	1	1	1	1	?
19.	2	2	2	2	1	2	2	*2*-3	2	2
20.	br	br-b	br-b	o-br?	br	po	po	*po*-o	b	?
21.	0	0	1	0	1	0	0	0	0	0?
22.	y	y	y-*g*	bl	?	w-y	w-y	bl-y	bl	?

Table (continued)

Characters	continua	interrupta		divus	caudata	similis		agilis	varia	mexicana
	♀	♀	♂	♀	♂	♀	♂	♀	♀	♀
23.	b	b	ybr-b	b	os	b	b	b	b	br
24.	a-dwp	a	a	a	a?	a	a	a	dwp	?
25.	e	a-e	a	e	?	e	a-e	a	a-e	?
26.	ni	ni	ni	ni-ns	?	ni	ns	ni-ns	ni	?
27.	1	1	1	1	1	1	1	1	1	?
28.	1	1	1	1	1?	1-2+	1	1	1-2+	?
29.	ne	ex	ne-ex	ex-ne	?	ex	ex	ex	ex	?
30.	2	2	2	2	2	2	2	2	2-9	4
31.	o-br	o-br	o-b	br-b	br?	b	br-b	obr-b	br-b	o?
32.	1-3	1	1	a	1-2?	a-1-2	1	a-1-2	a	?
33.	8-10	8-12	7-8	6-12	5+	9-17	4-6	6-10	6-14	?
34.	5.7	4.8	7.5	6.0	11.0?	5.9	6.1	5.5	6.3	6.5
35.	8.0	7.2	7.7	9.0	---	8.3	7.0	8.2	7.8	---
36.	122	173	3	197	0	105	2	286	10	0

Table (continued)

Characters	*major*		*flavipes*	*majuscula*	*venteris*		*insolita*	*apicalis*		*fasciata*
	♀	♂	♂	♂	♀	♂	♀	♀	♂	♀
1.	w	w	w	w	w	w	w	w	w	w
2.	2	2	?	?	1-2	1-2	3	1-2	1-2	2-3
3.	e	e	?	e	e	e	e?	e	e?	e
4.	o-obr	o-obr	br?	o-br	y-obr	o	o	yo	yo?	o-br
5.	1	1	1	1?	1	1	1	1	1	1-2-3
6.	1	1	1	1	1	1	1	1	1	1-2
7.	ea	ea	?	?	ea	ea	?	ne	ne?	ne
8.	sbs	sbs	u?	?	u	u	u	u	u	u
9.	n	n-e	n-e	e	a-n	n	n	a	a	a-n
10.	bb	bb	b?	bb?	bb	bb	bb	bb	bb	bb
11.	3	3	3	?	3	2-3	3	2	2	2
12.	w-y	w-y	?	?	w-y	w-y	b	b	b	b
13.	b	b	?	?	a-w-b	a-w-y	?	b	b?	a-b
14.	b	b	b	w-y	b	b	b	b	b	b
15.	o-obr	o	o?	y? o?	y-o	y	o?	o-obr	o?	o-br
16.	w-y-b	w-y-b	?	?	w-y-b	w-y	?	b	?	b
17.	25-50	20-30	?	?	5-30	5-10	?	35-55	?	25-35
18.	1	1	1	1	1	1	1	1	1	0
19.	2	2	?	?	2	1	?	2	2?	2
20.	po	po	po	o	o-ybr	y-ybr	po-o?	po	po	po
21.	0	1	2	1, 2?	0	1	0	0	0	0
22.	bl	w-y	?	?	y-g	g	?	bl	?	w-y

Table (continued)

Characters	major		flavipes	majuscula	venteris		insolita	apicalis		fasciata
	♀	♂	♂	♂	♀	♂	♀	♀	♂	♀
23.	b	o-os	os	ys	os	o	?	b	b	br-b
24.	a	a	a?	?	a	a	?	a	a	a
25	a	a	?	?	a	aa	?	a	a?	a
26.	ns	ns	?	?	ni-ns	ni	?	ni-ns	?	ni-ws
27.	1	1	1	1	1	1	1	1	1	1
28.	1	1	?	1?	1	1	?	1	1?	1-2+
29.	ex	ex-ne	?	?	ne-ex	ne	?	ne	?	ne
30.	2	2	2	2	2	2	2	2	2	2
31.	br-b	o-brb	?	?	obr-b	o	?	br-b	br-b	o-b
32.	a-1-2	1-3	?	?	1-3	1	?	4	4	1-3
33.	5-11	6-7	row	row	6-10	6	4	2-4	2	7-14
34.	6.8	8.8	9.6	10.0	5.3	8.2	7.5	6.9	8.0	4.0
35.	8.9	9.2	---	---	8.6	8.3	---	7.5	8.5	6.7
36.	43	2	0	0	441	2	0	2	0	244

Table (continued)

Characters	*bella*		*bequaerti*	*panamensis*		*valera*	*fumosa*	*aldrichi*	*townsendi*	*fulvibasis*
	♀	♂	♀	♀	♂	♂	♀	♀	♀	♀
1.	w	w	w	w	w	w	b	b	w	w
2.	1-2	2	4	4	4	4	4	3?	4	2-3?
3.	e	e	e	e	e?	e?	e	e?	e?	e?
4.	o-br	o-br	br	o-br	o-br	o-br	o-br	br?	b?	br?
5.	1-2	2	2	2-3	2	3	2-3	1	0	0
6.	1-2	1	3	3	3	3	1	1	0	0
7.	ne	ne	ea	ea	?	?	ea	ea	ne?	?
8.	u	u	u	u	u	u	u	u	u	sel
9.	a	a	n	n-e	n-e?	a	a	a?	a?-u?	n-e?
10.	bb	bb	bb	bb	bb	bb	b	b	b?	bb?
11.	2	2-3	3	3	3	3?	2-3	3	3	3
12.	b	b	b	b	b	b	b	b	b	b
13.	a-b	a-b	b	b	b	b	a-b	a?-b?	b	b
14.	b	b	b	b	b	b?	b	b?	b?	b?
15.	br	br	br	o-br	?	?	ybr	br?	b	?
16.	b	b	b	b	b	b	b	b?	b	b?
17.	35-45	35-45	25-35	25-35	?	?	15-25	?	?	?
18.	1	1	1	1	1	1	0	0	1	1
19.	2	1	2	2	?	?	1-2	?	1	?
20.	br	br	br	br	br	b?	ybr	?	b	po
21.	0	0	0	0	?	?	0	0	?	?
22.	w	y-g	w	w-y	y?	w?	w-bl	?	bl?	w?

Table (continued)

Characters	*bella*		*bequaerti*	*panamensis*		*valera*	*fumosa*	*eldrichi*	*townsendi*	*fulvibasis*
	♀	♂	♀	♀	♂	♂	♀	♀	♀	♀
23.	b	y-br	b	b	y-br	br	br-b	br-b?	b	b
24.	a	a	a	a	a?	a?	a	a?	a?	a?
25.	a	a	a	a	a?	a?	a	?	a?	a?
26.	ni	ni-ns	ni	ni	?	?	ws	?	?	ns-ws
27.	1	1	1	1	1	1	1	row	1	1
28.	1	1	1	1-2	?	?	1-2+	?	?	?
29.	ne	ne	ne-ex	no-ex	?	?	ne	ne	?	?
30.	2	2	2	2	2	2	2	2	2	2
31.	b	o-brb	br	br-b	?	?	obr	?	br?	br?
32.	4	4	a	a	1	2	4	4	1-3?	1-3?
33.	4-6-8	2-7	9-12	8-14	row	row	4-10	5+	6	4
34.	4.0	5.3	4.5	4.1	4.5	8.0	3.1	5.2	6.0	6.0
35.	6.4	6.8	---	6.1	7.0	---	4.5	---	---	---
36.	56	4	1	29	0	0	84	0	0	0

Table 9. Summary of Notochaeta Collection Records

Species of *Notochaeta*	Taken near ant species:						Not taken near ants		Totals	
	L. praedator		*E. burchelli*		*E. vagans*					
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
amphibiae [1]	2	-	5	1	2	-	-	-	9	1
bisetosa	1	3	4	2	-	-	-	1	5	6
frontalis	-	-	3	-	-	-	-	-	3	-
fuscianalis	1	-	-	-	-	-	-	3	1	3
monochaeta	-	-	-	2	-	-	-	-	-	2
palpalis	2	12	12	10	9	-	1	-	24	22
panamensis	1	-	-	-	-	-	-	-	1	-
not determined	1	6	-	55	-	-	-	-	-	61
Totals	7	21	24	70	11	-	1	4	43	95

[1] Reared specimens of *N. amphibiae* are not included in the above table.

Table 10. Gamasina Found with Ecitonini

Species of Gamasina	Species of Host							
	E. burchelli foreli	*E. burchelli urichi*	*E. burchelli cupiens*	*E. quadriglume*	*E. hamatum*	*E. dulcius*	*E. vagans*	*E. mexicanum*
Parasitoidea sp. A-1	1058 14c	1 1c	52? 1c	-	-	-	-	-
Parasitoidea sp. A-2	-	-	18? 1c	-	-	-	-	-
Macrochelidae sp. 2	-	-	-	-	-	23 3c	-	-
Macrochelidae sp. 3	-	-	-	-	-	-	57 4c	-
Macrochelidae sp. 7	-	1 1c	3 1c	-	-	-	-	-
Neoparasitidae sp. A-1	925 14c	1 1c	126 1c	-	72 10c	-	-	-
Neoparasitidae sp. A-2	-	-	-	-	-	5 1c	14 1c	-
Neoparasitidae sp. A-3	-	-	-	-	-	-	-	-
Neoparasitidae sp. A-4	-	-	-	-	-	-	-	-
Neoparasitidae sp. A-5	-	-	-	2 ?	-	-	-	-
Neoparasitidae sp. A-6	-	-	-	-	-	-	-	-
Laelaspis sp. 1	-	-	-	-	-	-	-	-
Laelaspis sp. 2	1 1c	-	-	-	-	-	-	-
Laelaspis sp. 3	-	-	-	-	12 1c	-	-	-
Laelaspis sp. 4	-	-	-	-	-	-	-	2 1c
Laelaspis sp. 5	1 1c	-	-	-	-	-	-	-
Laelaspis sp. 6	-	-	-	-	-	-	-	-
Laelaspis sp. 7	-	-	-	-	-	-	-	-
Laelaspis sp. 8	-	-	-	-	-	-	-	-
Laelaspis sp. 9	-	-	2 1c	-	-	-	-	-
Laelaspis sp. 10	-	-	1 1c	-	-	-	-	-
Total	1985	3	202	2	84	28	71	2

Table 10 (continued). Gamasina Found with Ecitonini

Species of Gamasina	Species of Host						
	Labidus praedator	*L. coecus*	*Nomamyrmex esenbecki*	Neiv. *gibbatus*	Neiv. *harrisi*	*Eciton* total	Total
Parasitoidea sp. A-1	1 1c	-	-	-	-	1111 16c	1112 17c
Parasitoidea sp. A-2	-	-	-	-	-	18 1c	18 1c
Macrochelidae sp. 2	-	-	-	-	-	23 3c	23 3c
Macrochelidae sp. 3	-	-	-	-	-	57 4c	57 4c
Macrochelidae sp. 7	-	-	-	-	-	4 2c	4 2c
Neoparasitidae sp. A-1	-	-	-	-	-	1124 26c	1124 26c
Neoparasitidae sp. A-2	-	-	-	-	-	19 2c	19 2c
Neoparasitidae sp. A-3	26 2c	-	-	-	-	-	26 2c
Neoparasitidae sp. A-4	2 2c	-	59 1c	-	-	-	61 3c
Neoparasitidae sp. A-5	-	-	-	-	-	2 ?	2 ?
Neoparasitidae sp. A-6	-	-	-	-	11 ?	-	11 ?
Laelaspis sp. 1	15 5c	-	-	-	-	-	15 5c
Laelaspis sp. 2	-	-	-	-	-	1 1c	1 1c
Laelaspis sp. 3	-	-	-	-	-	12 1c	12 1c
Laelaspis sp. 4	-	-	-	-	-	2 1c	2 1c
Laelaspis sp. 5	-	-	-	1 1c	-	1 1c	2 2c
Laelaspis sp. 6	-	-	36 1c	-	-	-	36 1c
Laelaspis sp. 7	-	-	31 2c	-	-	-	31 2c
Laelaspis sp. 8	-	7 1c	-	-	-	-	7 1c
Laelaspis sp. 9	-	-	-	-	-	2 1c	2 1c
Laelaspis sp. 10	-	-	-	-	-	1 1c	1 1c
Total	44	7	126	1	11	2377	2566

Table 11. Uropodina Found with Ecitonini

Species of Uropodina	Species of Host								
	E. burchelli foreli	*E. burchelli urichi*	*E. burchelli cupiens*	*E. burchelli burchelli*	*E. quadriglume*	*E. hamatum*	*E. dulcius*	*E. vagans*	*E. mexicanum*
Planodiscus squamatus	-	-	-	9 1c	7 1c	-	-	-	-
Planodiscus sp. A-2	221 10c	-	-	-	-	-	-	-	-
Planodiscus sp. A-3	-	-	56 1c	-	-	-	-	-	-
Planodiscus sp. A-4	-	-	45 1c	-	-	-	-	-	-
Planodiscus sp. A-6	-	-	-	-	-	-	-	-	7 3c
Planodiscus sp. A-9	-	-	-	-	-	-	-	1 1c	-
Planodiscus sp. B-1	919 15c	1 1c	19 1c	-	-	-	-	2 1c	-
Planodiscus sp. B-5	-	-	-	-	-	199 17c	-	2 1c	-
Planodiscus sp. B-7	-	-	-	-	-	35 6c	4 2c	-	15 5c
Planodiscus sp. B-8	-	-	-	-	-	-	-	3 1c	-
Planodiscus sp. B-10	-	-	-	-	-	-	-	-	-
Circocylliba sp. 1	400 11c	-	-	-	-	143 16c	7 2c	1 1c	5 3c
Circocylliba sp. 2	54 6c	-	-	-	-	-	-	-	7 4c
Circocylliba sp. 3	-	1 1c	2 1c	-	-	-	-	-	-
Circocylliba sp. 4	-	-	-	-	-	-	29 4c	9 5c	-
Circocyllibanidae sp. A-1	-	-	-	-	-	5 2c	-	-	-
Circocyllibanidae sp. B-1	-	-	-	-	-	-	-	-	-
Circocyllibanidae sp. B-2	-	-	-	-	-	-	-	-	-
Circocyllibanidae sp. B-3	-	-	-	-	-	-	-	-	-
Circocyllibanidae sp. C-1	-	-	-	-	-	-	-	-	-
Circocyllibanidae sp. D-1	-	-	-	-	-	-	-	-	-
Total	1594	2	122	9	7	382	40	18	34

Table 11 (continued). Uropodina Found with Ecitonini

Species of Uropodina	Species of Host				
	L. praedator	*L. coecus*	*Neiv. legionis*	*Eciton* total	Total
Planodiscus squamatus	-	-	-	16 2c	16 2c
Planodiscus sp. A-2	-	-	-	221 10c	221 10c
Planodiscus sp. A-3	-	-	-	56 1c	56 1c
Planodiscus sp. A-4	-	-	-	45 1c	45 1c
Planodiscus sp. A-6	-	-	-	7 3c	7 3c
Planodiscus sp. A-9	-	-	-	1 1c	1 1c
Planodiscus sp. B-1	-	-	-	941 18c	941 18c
Planodiscus sp. B-5	-	-	-	201 18c	201 18c
Planodiscus sp. B-7	-	-	-	54 13c	54 13c
Planodiscus sp. B-8	-	-	-	3 1c	3 1c
Planodiscus sp. B-10	-	-	1 1c	-	1 1c
Circocylliba sp. 1	-	-	-	556 33c	556 33c
Circocylliba sp. 2	-	-	-	61 10c	61 10c
Circocylliba sp. 3	-	-	-	3 2c	3 2c
Circocylliba sp. 4	-	-	-	38 9c	38 9c
Circocyllibanidae sp. A-1	-	-	-	5 2c	5 2c
Circocyllibanidae sp. B-1	24 3c	-	-	-	24 3c
Circocyllibanidae sp. B-2	-	76 5c	-	-	76 5c
Circocyllibanidae sp. B-3	-	2 1c	-	-	2 1c
Circocyllibanidae sp. C-1	-	1 1c	-	-	1 1c
Circocyllibanidae sp. D-1	1 1c	-	-	-	1 1c
Total	25	79	1	2208	2313

Table 12. Pyemotidae Found with Dorylinae

Species of Pyemotidae	Species of Host							
	Dorylus (*Anomma*)	*E. burchelli*	*E. hamatum*	*E. dulcius*	*E. vagans*	*E. mexicanum*	*L. praedator*	*L. coecus*
Acinogaster marianae	-	269 16c	51 5c	-	-	-	-	-
Acinogaster sp. 2	18 1c	-	-	-	-	-	-	-
Acinogaster sp. 3	-	-	-	4 2c	-	-	84 8c	6 3c
Acinogaster sp. 5	-	-	-	-	-	-	-	-
Acinogaster sp. 20	-	29 7c	-	5 2c	3 1c	11 3c	52 6c	2 2c
Acinogaster sp. 30	-	-	-	-	-	-	-	-
Myrmecodispus dorylinus	-	11 1c	-	-	220 5c	-	-	-
Myrmecodispus sp. 1	-	-	-	40 1c	18 4c	-	-	-
Myrmecodispus sp. 2	-	-	-	-	-	-	-	-
Myrmecodispus sp. 3	-	-	-	-	-	-	-	-
Myrmecodispus sp. 4	-	-	-	-	-	-	-	-
Perperipes ornithocephala	-	-	37 2c	-	-	-	-	-
Perperipes sp. 1	-	64 8c	-	-	-	-	-	-
Perperipes sp. 2	-	-	-	-	-	-	-	-
Species other than above	-	1 1c	-	7 3c	8 3c	2 2c	-	-
Species not determined	-	775	62	55	486	-	45	-
Total Pyemotidae	18	1149	150	111	735	13	181	8

c = number of colonies in which each species of mite was found.

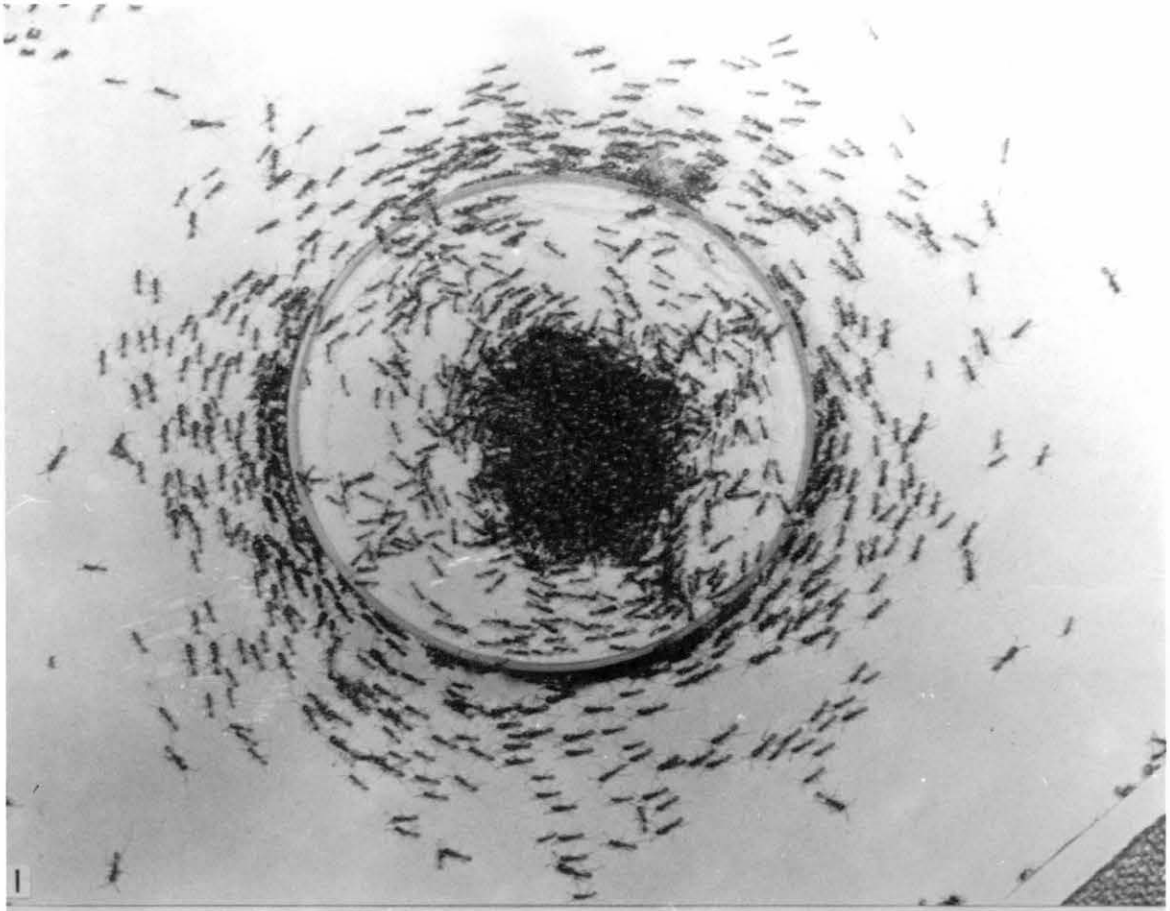
Table 12 (continued). Pyemotidae Found with Dorylinae

Species of Pyemotidae	Species of Host							
	Noma. esenbecki	*Noma. hartigi*	*Neiv. gibbatus*	*Neiv. pilosus*	*Neiv. legionis*	*Neiv. nigrescens*	*Neiv. opacithorax*	Total
Acinogaster marianae	-	-	-	-	-	-	-	320 21c
Acinogaster sp. 2	-	-	-	-	-	-	-	18 1c
Acinogaster sp. 3	2 1c	1 1c	1 1c	5 1c	1 1c	-	-	104 18c
Acinogaster sp. 5	-	-	-	-	4 1c	-	-	4 1c
Acinogaster sp. 20	4 1c	3 1c	2 1c	2 2c	2 1c	-	-	115 27c
Acinogaster sp. 30	-	-	-	-	-	13 2c	15 2c	28 4c
Myrmecodispus dorylinus	-	-	-	-	-	-	-	231 6c
Myrmecodispus sp. 1	-	-	-	-	-	-	-	58 5c
Myrmecodispus sp. 2	43 1c	-	-	-	-	-	-	43 1c
Myrmecodispus sp. 3	-	1 1c	-	-	-	-	-	1 1c
Myrmecodispus sp. 4	2 1c	-	-	-	-	-	-	2 1c
Perperipes ornithocephala	-	-	-	-	-	-	-	37 2c
Perperipes sp. 1	-	-	-	-	-	-	-	64 8c
Perperipes sp. 2	1 1c	-	-	-	-	-	-	1 1c
Species other than above	2 1c	2 1c	4 1c	-	5 1c	2 2c	2 1c	33 16c
Species not determined	-	-	-	-	2	240	14	1679
Total Pyemotidae	53	5	7	7	14	255	31	2737

Figure 1. Workers of *Neivamyrmex opacithorax* running clockwise in circular column around an uncovered petri dish 65 mm. in diameter. Moist blotter paper is in center of dish, and about two thirds of ants are clustered on top of it. No food nor brood is present. Dead ants are scattered around edges of nest (one edge visible in lower right corner). Column lasted for at least six hours but broke up when dish was removed from center.

Figure 2. Vertical laboratory nest with "ropes" of *Eciton hamatum* and large cluster of these ants hanging at right side. Water is supplied by capillary action from bottle by three 5 mm. diameter cotton cords seen at top left. Entrance tubing about 12 mm. in diameter is at lower left. Glass front and back are held tightly against foam rubber strips by wood blocks bolted to wood frame of nest. Light gray paper is behind nest.

1



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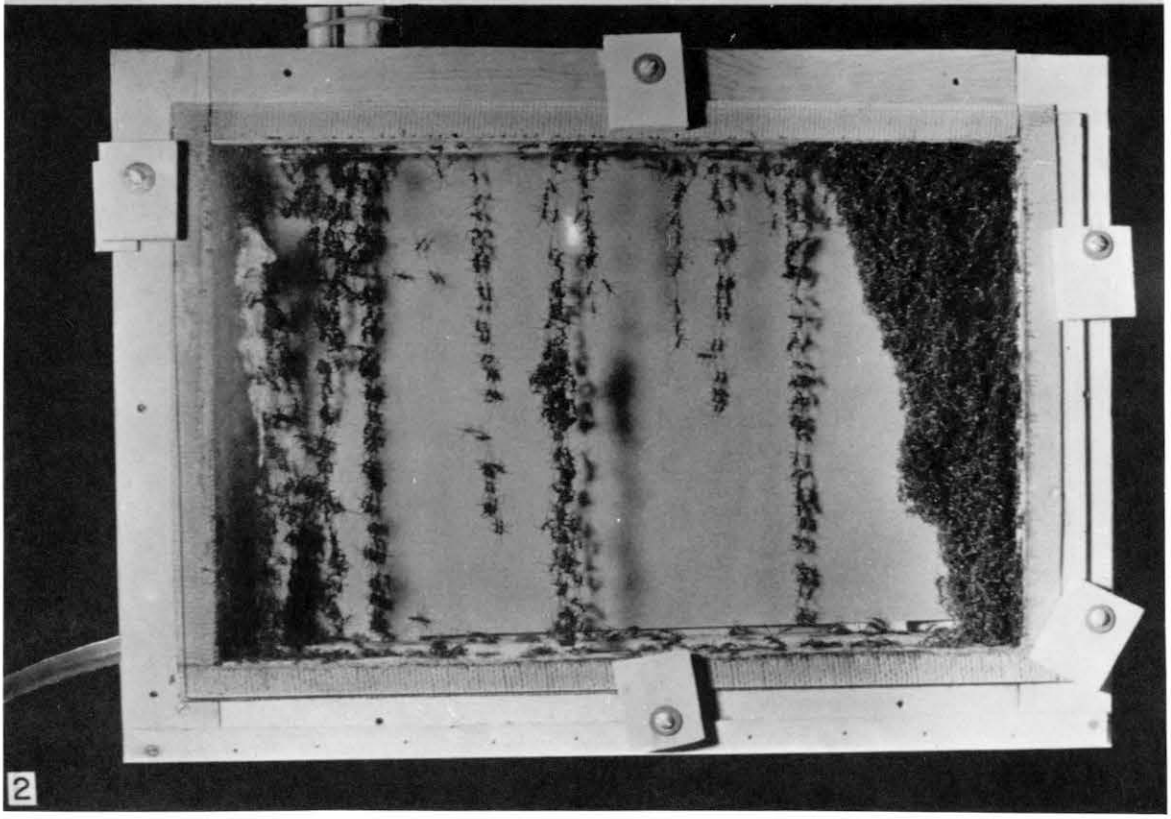
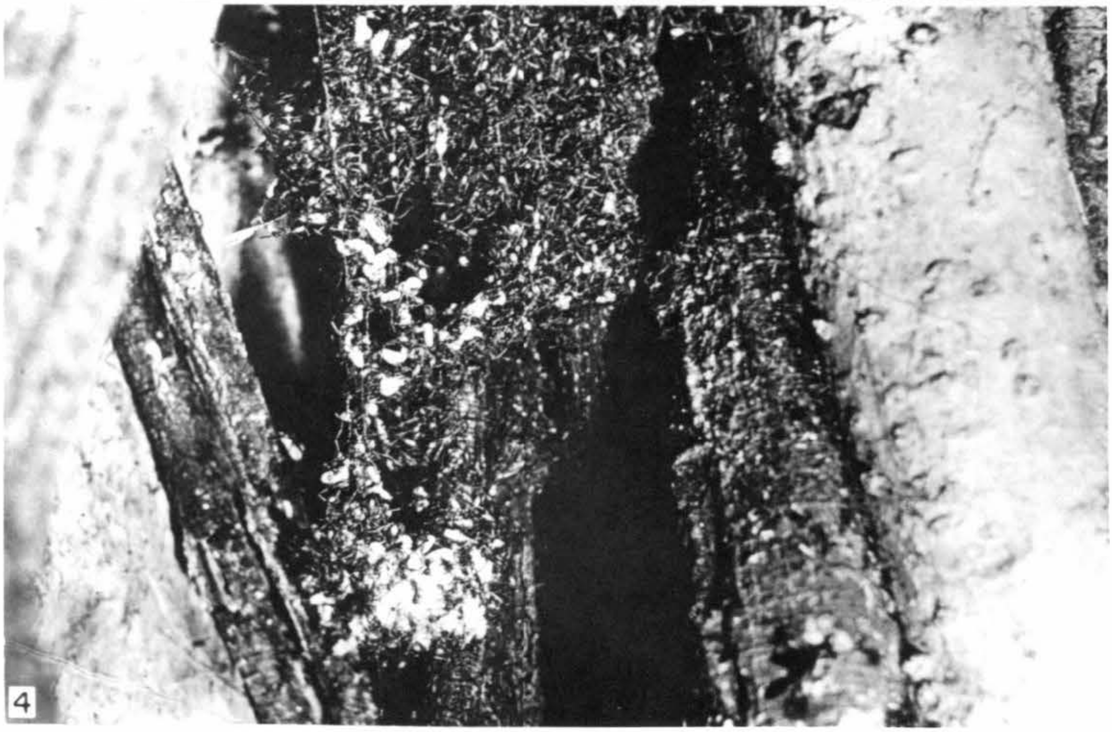


Figure 3. Bivouac (dark mass) of Eciton burchelli, colony E-253, between buttresses of large tree on 17 August 1956. Colony is in nomadic phase with worker larvae almost mature. Width of bivouac is about 45 cm.

Figure 4. Lower edge of bivouac of E. burchelli, colony '55 B-I, photographed on 5 February 1955 as ants were moving from this statary site in a large tree. White objects scattered among workers are empty cocoons which dropped to refuse deposit on ground when ants left.

3



4

Figure 5. Emigration column of _E. burchelli_ showing ants holding edges of leaves closer together with their legs. Bodies of ants form a bridge over which other workers are emigrating. Ants on right are carrying worker larvae and booty. (Colony E-222, 26 July 1956).

Figure 6. Emigration column of _E. burchelli_ across liana about ten millimeters in diameter. Ants have made flanges on each side of liana which have tripled width of "roadway" over which other ants can emigrate. These flanges extend along column for about one meter where the liana forms a bridge from a log (at right edge of picture) to a small tree (out of the picture on the left). (Colony E-253, 17 August 1956).

Figure 7. Close-up of emigration column with flanges in figure 6. Some ants are carrying worker-producing larvae which are held at one end by the mandibles of the workers. Army ants always carry objects under their bodies.

5

6

7

Figure 8. Walls of loose dirt and complete tunnel (near right side) made by Labidus praedator. Legs and other parts of "guard workers" can be seen between walls. Main emigration column between walls cannot be seen. (Colony E-177, 30 May 1956).

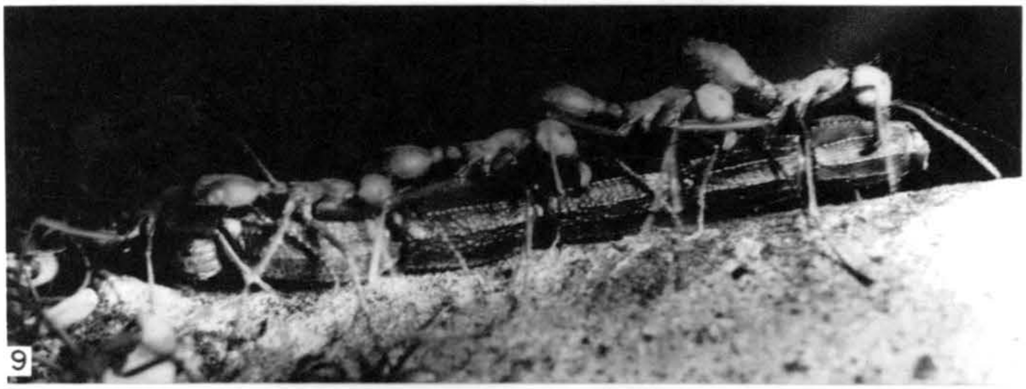
Figure 9. Tail of a scorpion being carried by three submajors and an intermediate worker of E. burchelli in raid column. A fifth worker at left end is partially riding on the tail but not helping to carry it. (Colony E-253, 17 August 1956).

Figure 10. Submajor of E. burchelli on right is carrying tergum and sternum of an orthopteran (cockroach?) while another worker is partially riding on the booty. Large worker behind it is carrying white wasp pupa. (Colony E-253, 17 August 1956).

Figure 11. Excited workers of Neivamyrmex opacithorax. Note open mandibles, antennae extended laterally and above head, and front legs off floor of nest. Maximally stimulated workers hold their bodies even more nearly vertical than worker on right. (Colony E-267, 23 Oct. 1959 in laboratory nest).

Figure 12. Large and small workers of Labidus coecus showing almost greatest size range and head enlargement within Ecitonini. (Colony E-201, 2 July 1956).


8


9


10


11


12

Figure 13. Close-up of part of refuse deposit next to nomadic bivouac of _E_. _burchelli_. Male phorid fly is at right of center. Abdominal terga of large black ants can be seen in lower left and right corners. Straight objects are mainly leg segments or antennae of orthopterans and ants. (Colony E-253, 16 Aug. 1956).

Figure 14. Emigration column of _Neivamyrmex_ _opacithorax_ in Lawrence, Kansas. Arrow indicates phorid fly which at instant of flash was running away from column. Phorids run in zigzag manner often darting into center of column and then out again. At least five ants are carrying larvae. (Colony E-266, 19 August 1959).

13

14

Figures 15 to 20. Mites on their hosts. Figures 15 to 18 are photographs of living specimens; figures 19 and 20 are of specimens in alcohol.

Figure 15. Distal segments of two hind tarsi of major workers of *E. dulcius crassinode*. Macrochelidae sp. 2 (2062) is attached to the membrane between the claws of the lower tarsus.

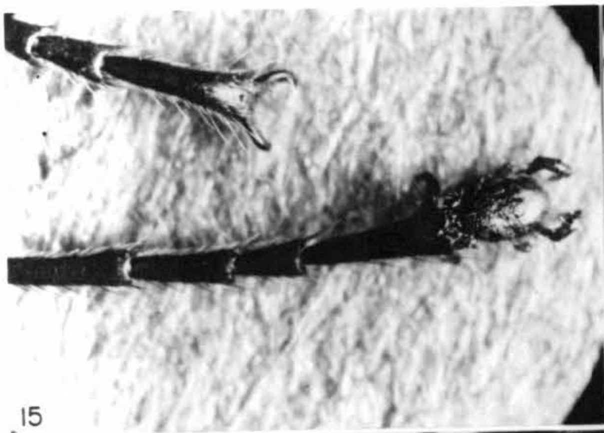
Figure 16. Intermediate worker and a larva of *E. hamatum*. *Planodiscus* sp. B-5 is riding on the underside of the left hind leg. *Circocylliba* sp. 1 is riding on the abdominal terga and three specimens are on the larva. (All specimens 1999)

Figure 17. Major worker of *E. dulcius crassinode* with *Circocylliba* sp. 4 riding on each mandible (Colony E-204).

Figure 18. Same species as figure 17 showing long dorsal setae of mite and its position on medial, concave surface of mandible (Colony E-204).

Figure 19. Posterior view of Coxequesomidae sp. B-1 on scape of large worker of *Nomamyrmex esenbecki crassicornis* (1826).

Figure 20. Same specimen as figure 19, showing mite in lateral view.



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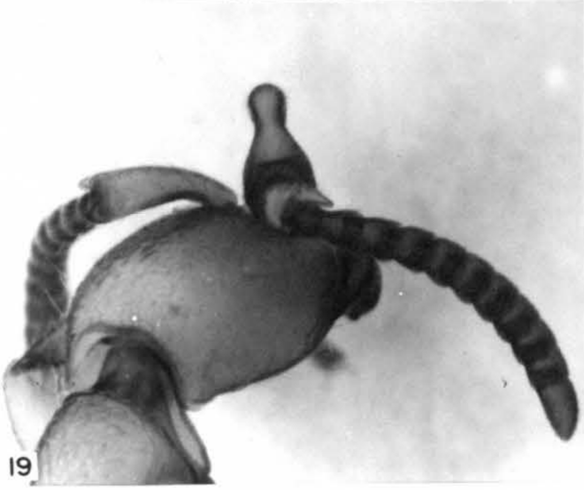

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Figures 21 to 26. Larviform mites and associated ant eggs and larvae. Figures 21, 22 and 24 are photographs of living specimens; figures 23, 25a and 26a are of specimens in alcohol.

Figure 21. *Larvimima* sp. (2101) walking on small larva of *E. hamatum*.

Figure 22. Lateral view of same specimen in figure 21. Note small size of four pair of legs at right end of specimen. Opisthosoma shows two distinct small anterior "segments" followed by a third indistinct small segment and a much larger posterior segment.

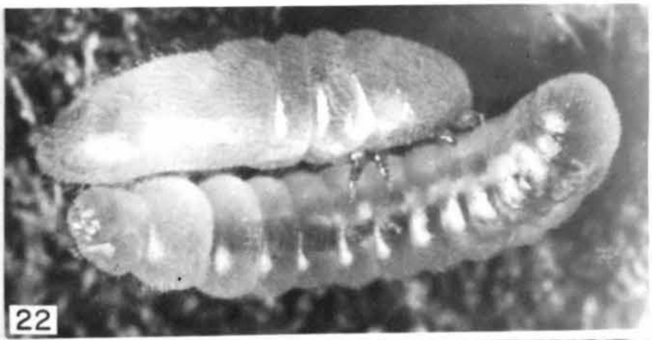
Figure 23. Dorsal view of *Larvimima* sp. 4, third specimen from left (1547-A). All other specimens are *E. hamatum* larvae with which the mite was found.

Figure 24. Ventral view of specimen shown in figures 21 and 22. Mite is unable to right itself when turned on its back. Note pile-like covering of uniform setae on all sides of mite and absence of sclerotized plates.

Figure 25. *Larvimima* sp. 2 with eggs and larvae of *E. hamatum* with which mites were found (colony '48 H-D from Darien Prov., Panamá taken by T. C. Schneirla). In figure 25b the ant brood is stippled.

Figure 26. Gravid females of pyemotid, *Acinogaster marianae* (1426) with larvae of *E. burchelli foreli* with which they were found. Ant brood is stippled in figure 26b.


21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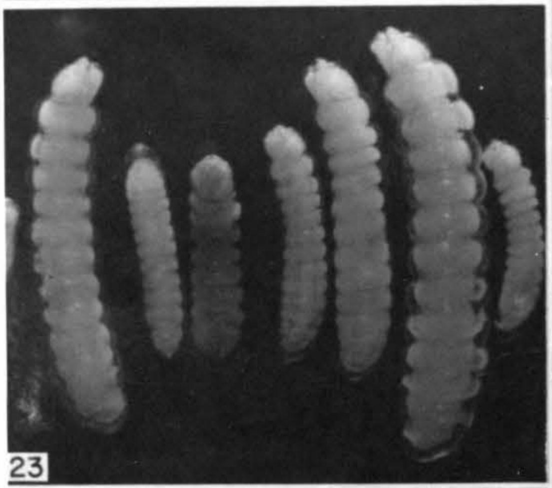
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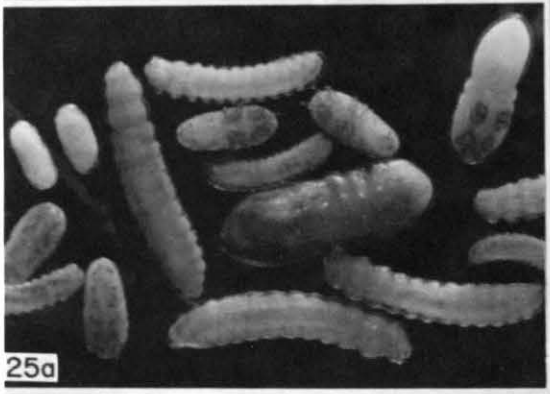
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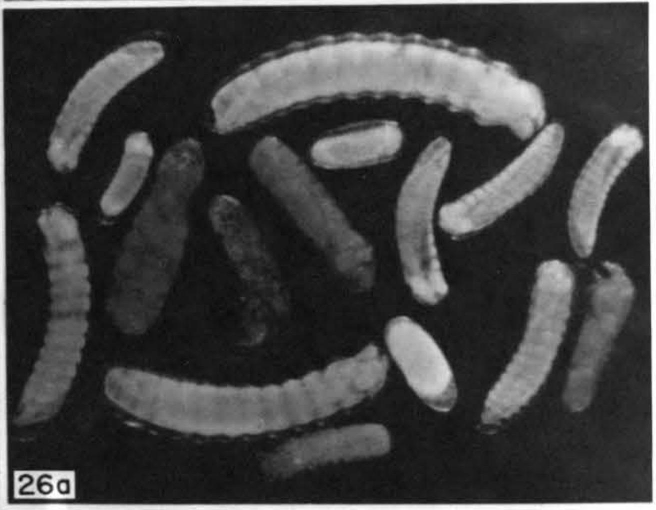
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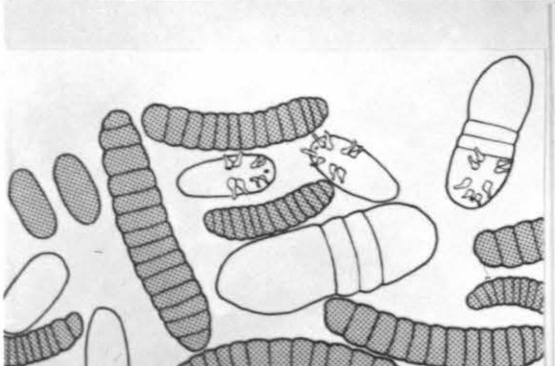
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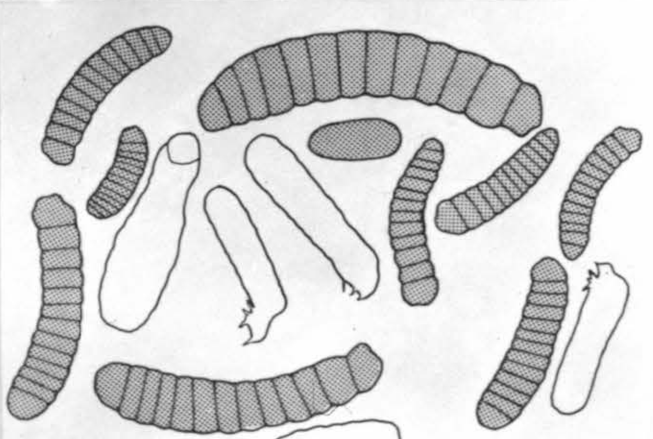
26b

Figure 27. *Calymmodesmus gracilis* or *C. rettenmeyeri* on right running in center of emigration column of *L. praedator*. Anterior end frequently is turned up in this manner as millipeds run along in columns. (1876, Colony E-177, 30 May 1956).

Figure 28. *Rettenmeyeria parvipes* in laboratory nest. (1786, Colony E-164. 19 May 1956).

Figure 29. Dorsal view of *Calymmodesmus* or *Rettenmeyeria* in laboratory nest. (1814, Colony E-164, 18 May 1956).

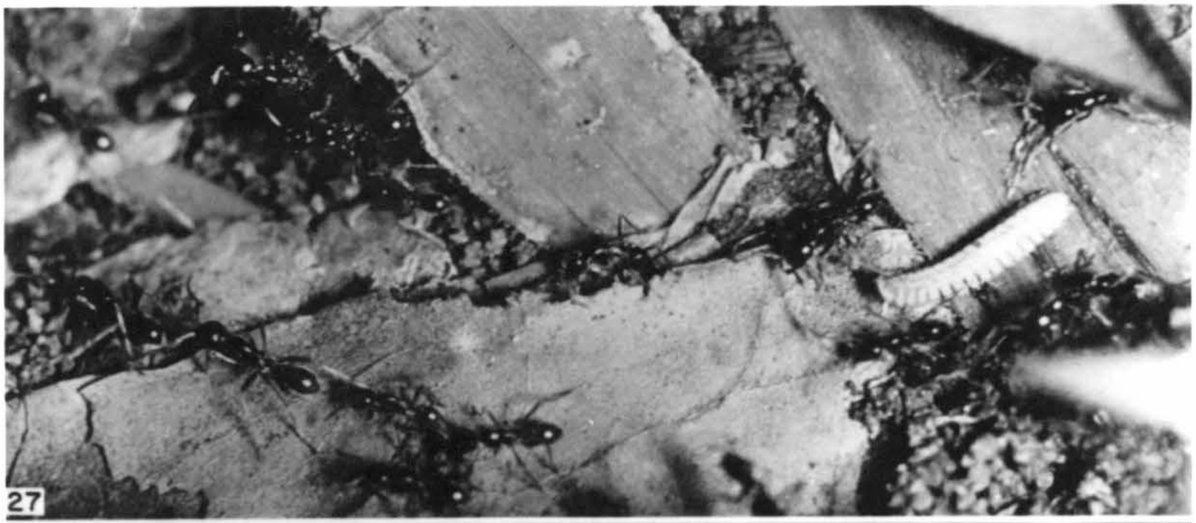
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Figure 30. *Grassiella rettenmeyeri* (Thysanura: Nicoletiidae) photographed in laboratory nest. When thysanuran runs, anterior end is held higher. (2010, Colony E-194, *E. dulcius*, 23 June 1956).

Figures 31 to 38. *Trichatelura manni*. (Nicoletiidae).

Figure 31. *T. manni* running in center of emigration column of *E. burchelli* (Colony E-222, 26 July 1956).

Figure 32. *T. manni* raising and flipping its abdomen which dislodged tarsus of worker. (Colony E-204, *E. dulcius*, 4 July 1956).

Figure 33. Dorsolateral view of running thysanuran. In figures 33, 34 and 37 note that legs are kept greatly extended laterally, and thysanuran runs on tips of tarsi. Abdominal styli are pointed straight down, cerci turn upward, palpi down. (2003, Colony E-192, *E. hamatum*, 23 June 1956).

Figure 34. Lateral view. (1241, Colony E-107, *E. burchelli*, 24 February 1956).

Figures 35 and 36. *T. manni* climbing on thorax and head of major worker of *E. dulcius*. (Colony E-204, 4 July 1956).

Figure 37. *T. manni* shown running after worker of *E. hamatum* which had just turned sharply to left, and thysanuran is turning after it. (Colony E-191, 24 June 1956).

Figure 38. Feeding on booty among workers of *E. dulcius*. (Colony E-204, 4 July 1956).


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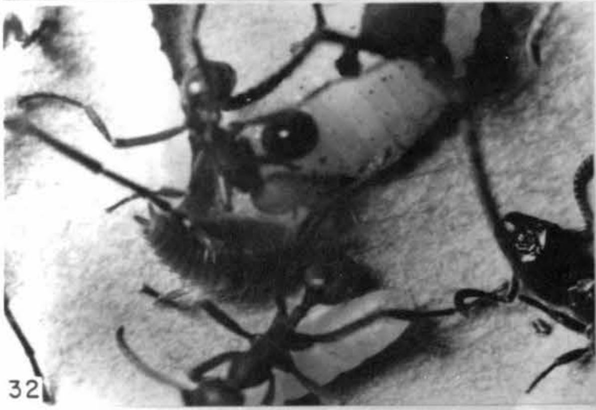
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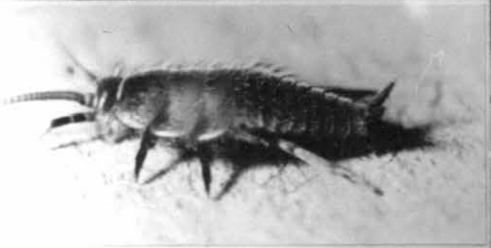
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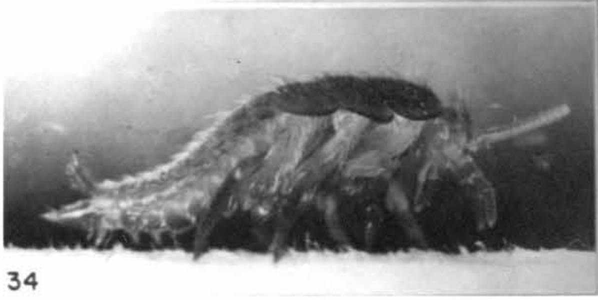
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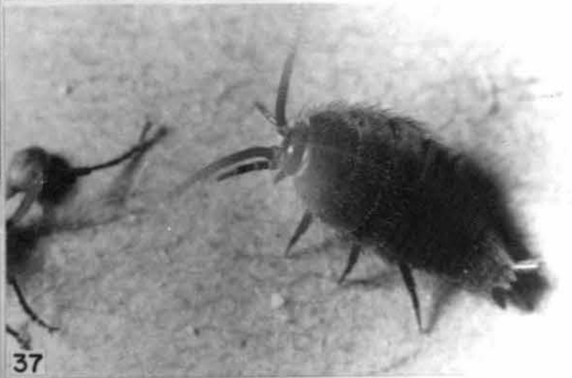
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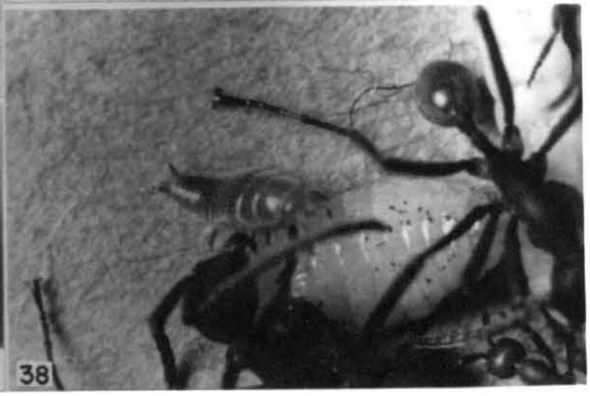
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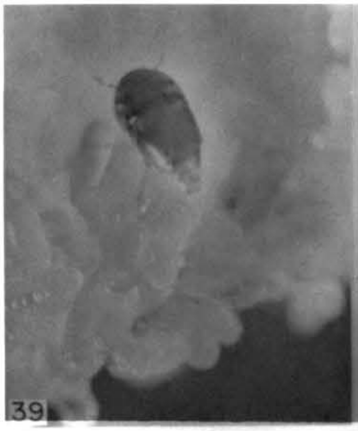
Figure 39. *Cephaloplectus mus* (Limulodidae) on eggs and young larvae of *E. burchelli* during fourth nomadic day. (1675-B, Colony E-136, 26 April 1956). Note that all living specimens have antennae extended in front of head, and long tapering abdomen is usually not pulled in (as is common with dead specimens).

Figure 40. *Cephaloplectus* sp. riding on first gaster segment of queen *E. dulcius*. At least seven specimens of this species were on this queen when she was picked out of emigration column. Additional specimens were running in column, and two were seen on major workers. (1594, Colony E-137, 3 April 1956).

Figure 41. *Cephaloplectus* sp. riding on queen of *Nomamyrmex esenbecki crassicornis*. At least 21 of this species of beetle were clinging to this queen when she was running in an emigration column. (1831, Colony E-164, 18 May 1956).

Figure 42. Diagram traced from figure 41 to show positions of 14 limulodids on queen and one on floor of laboratory nest.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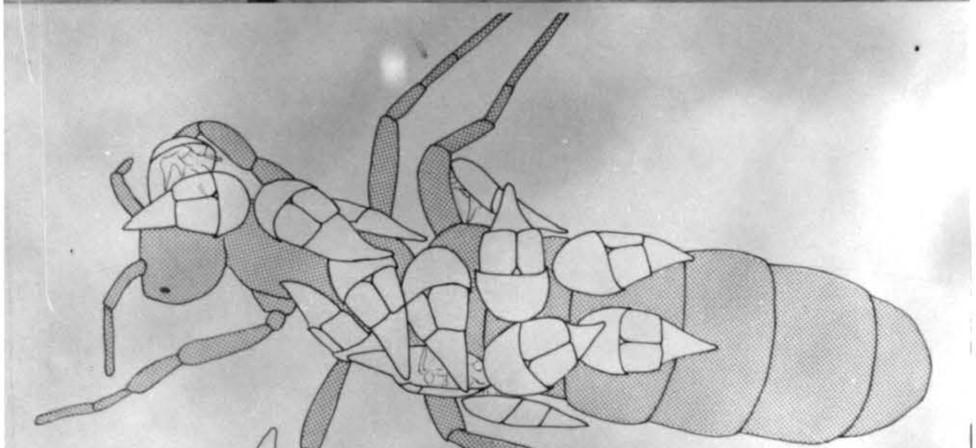
42

Figures 43 to 49. In these photographs the beetles which are attacking workers have their abdomens curved toward the ants. These staphylinids can emit a substance from the tips of their abdomens which repels and possibly stuns the ants.

Figure 43. Tetradonia prosequens attacking worker of Eciton hamatum which is almost dead. (1998, Colony E-191, 20 June 1956).

Figure 44. ?Mimeciton antennatum. Note long legs and abdomen modified like gaster of ant. (Colony E-183, Labidus praedator, 5 June 1956).

Figures 45 to 47. Staphylinid (genus near Zyras) attacking worker of Nomamyrmex esenbecki. (2132, Colony E-215, 18 July 1956).

Figure 45. Staphylinid pulling ant backward by ant's hind leg.

Figures 46 and 47. Staphylinids feeding at joints of legs.

Figure 48. Ecitomorpha nevermanni. (Colony E-107, 24 February 1956).

Figure 49. Same species as in figures 45 to 47. Abdomen is held straight or slightly curved when beetle is not attacking ants.


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Figures 50 to 54. *Vatesus panamensis* (Staphylinidae).

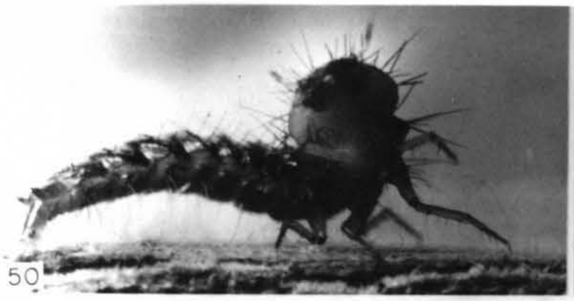
Figure 50. Larva with head and prothorax turned up against glass side of laboratory nest. Head of larva can be pulled under pronotum. Pygopod at tip of abdomen is used to hold to substrate. (1530, Colony E-121, *E. hamatum*, 18 March 1956).

Figure 51. Larva with head extended. Long setae extending in all directions may be protective adaptation against attacks by ants (?). (1963, Colony E-168, *E. hamatum*, 13 June 1956).

Figure 52. Inactive prepupa. Curved position with legs drawn close to body was typical for all prepupae of this species. (same specimen [?] as in figure 51, larva found 13 June 1956, photographed 20 June 1956).

Figure 53. Pupa starting to become dark. (same specimen [?] as in figure 50, photographed on 26 March 1956).

Figure 54. Adult in center of emigration column of *E. burchelli*. (Colony E-253, 16 August 1956).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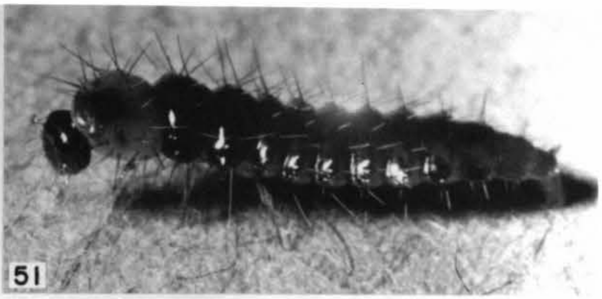
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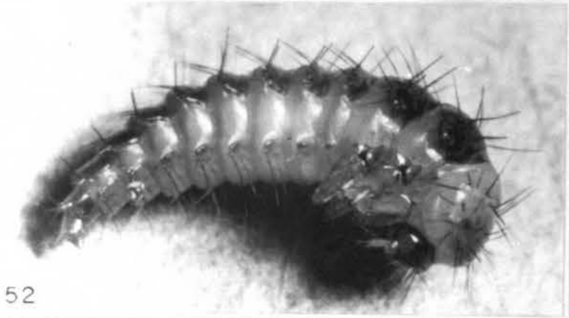
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Figure 55. *Euxenister caroli* showing unusually long legs and carinae along dorsolateral edges of abdomen and thorax compared with nonmyrmecophilous Histeridae. Staphylinid at upper left is *Ecitomorpha nevermanni*. (Colony E-107, *E. burchelli*, 23 February 1956).

Figure 56. *Euxenister caroli* riding on thorax of medium-sized intermediate worker of *E. burchelli*. Note how hind leg of beetle extends behind and partially under hind leg of ant and would appear to hinder running by worker.

Figures 57 to 60. *Latronister rugosus* climbing on large worker of *E. vagans*. Same individuals are in all photographs. Worker stood quietly as beetle climbed around on it and grasped ant's antenna with mandibles (figure 60). No injuries to ant or beetle were apparent. (2167 or 2199, Colony E-219, 26 July 1956).


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Figure 61. Egg of <u>Stylogaster currani</u> Aldrich inserted in membrane between first and second abdominal terga on right side of <u>Calodexia agilis</u> Curran female (2329-A).

Figure 62. Egg of <u>Stylogaster minuta</u> Townsend inserted in ventrolateral part of eye of <u>Calodexia agilis</u> Curran female (1446-C).

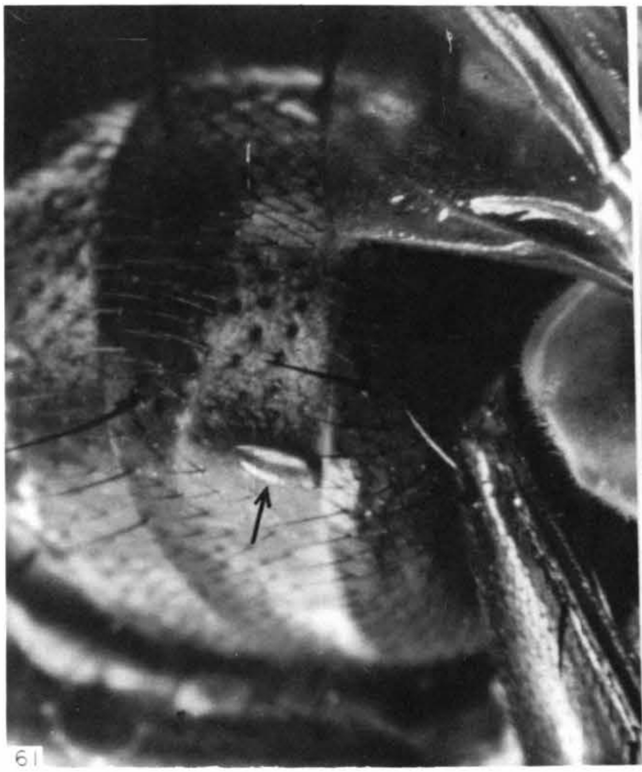

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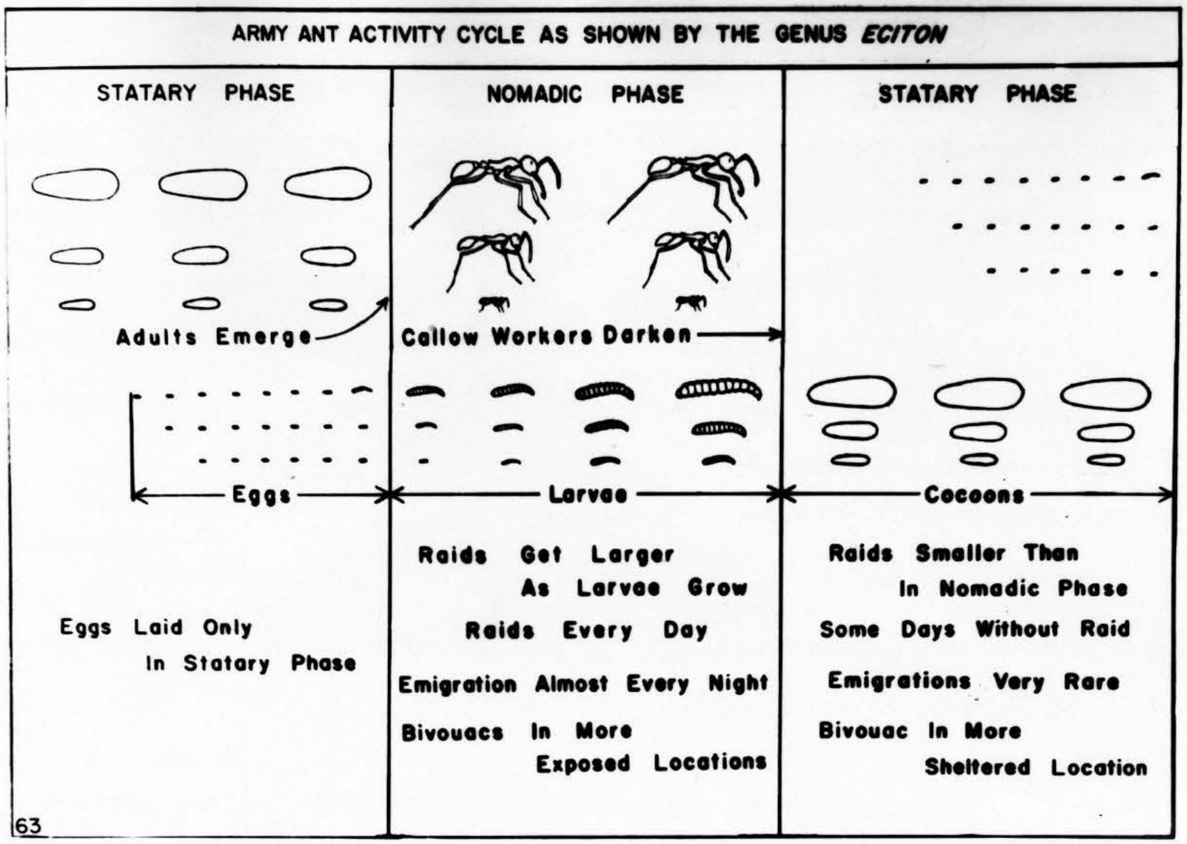
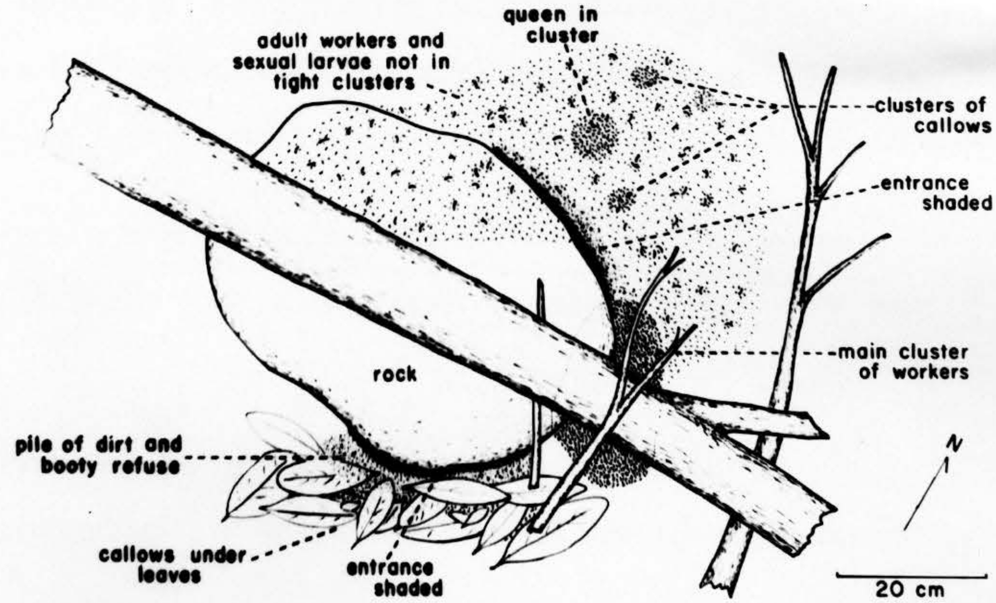
Figure 63. Main features of army ant activity cycle based on behavior of *Eciton hamatum* as determined by Schneirla.

Figure 64. Diagram of bivouac of colony E-212, *Eciton vagans*, as it was found about 11:30 a. m., 9 July 1956. Numerous leaves and small twigs which covered entire area are not shown. Diagram indicates positions of workers hanging in one main cluster and dispersed under leaves on top of rock and around its north, east and south edges; sexual larvae scattered among workers, but absent in hanging cluster; callow workers primarily in two distinct clusters and scattered at south edge of bivouac; queen under leaves and twigs on surface of ground in small cluster of workers not including callows. Entrances on north and southeast edges of rock led to shallow cavities with scattered workers. (Cavities were possibly filled with workers before large number of raiding ants had left bivouac.) Refuse from booty was scattered mainly along southeast edge of rock with dirt excavated from under rock.


ARMY ANT ACTIVITY CYCLE AS SHOWN BY THE GENUS *ECITON*
STATARY PHASE
NOMADIC PHASE
STATARY PHASE
Adults Emerge
Callow Workers Darken
Eggs
Larvae
Cocoons
Eggs Laid Only In Statary Phase
Raids Get Larger As Larvae Grow
Raids Every Day
Emigration Almost Every Night
Bivouacs In More Exposed Locations
Raids Smaller Than In Nomadic Phase
Some Days Without Raid
Emigrations Very Rare
Bivouac In More Sheltered Location

63


queen in cluster
adult workers and sexual larvae not in tight clusters
clusters of callows
entrance shaded
main cluster of workers
rock
pile of dirt and booty refuse
callows under leaves
entrance shaded
N
20 cm

64

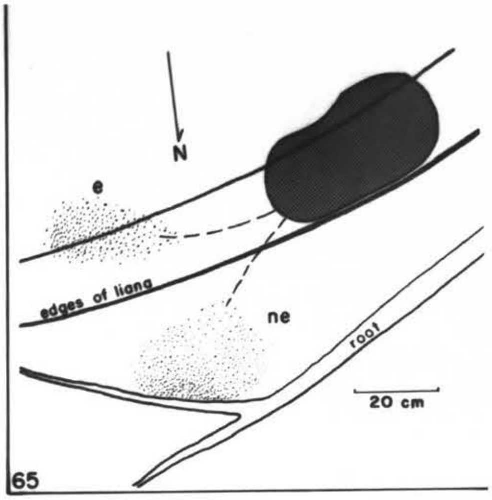
Figures 65 to 68. Diagrams of refuse deposits of <u>Eciton</u> <u>burchelli</u>. All drawn as if viewed perpendicularly from above bivouacs which are heavily stippled. Solid lines ending in arrows are raid and/or emigration columns, dashed lines are refuse columns. Thickness of lines indicates estimated use by ants. Stippling along refuse columns indicates position and estimated relative amounts of refuse with most distinct areas of refuse indicated by letters and numbers.

Figure 65. Nomadic bivouac with refuse deposit <u>e</u> hidden from above under liana and in shallow cavity in soil. Refuse deposit <u>ne</u> exposed from above and with distal edge against root. (Colony '55 B-IV-N, 11 March 1955).

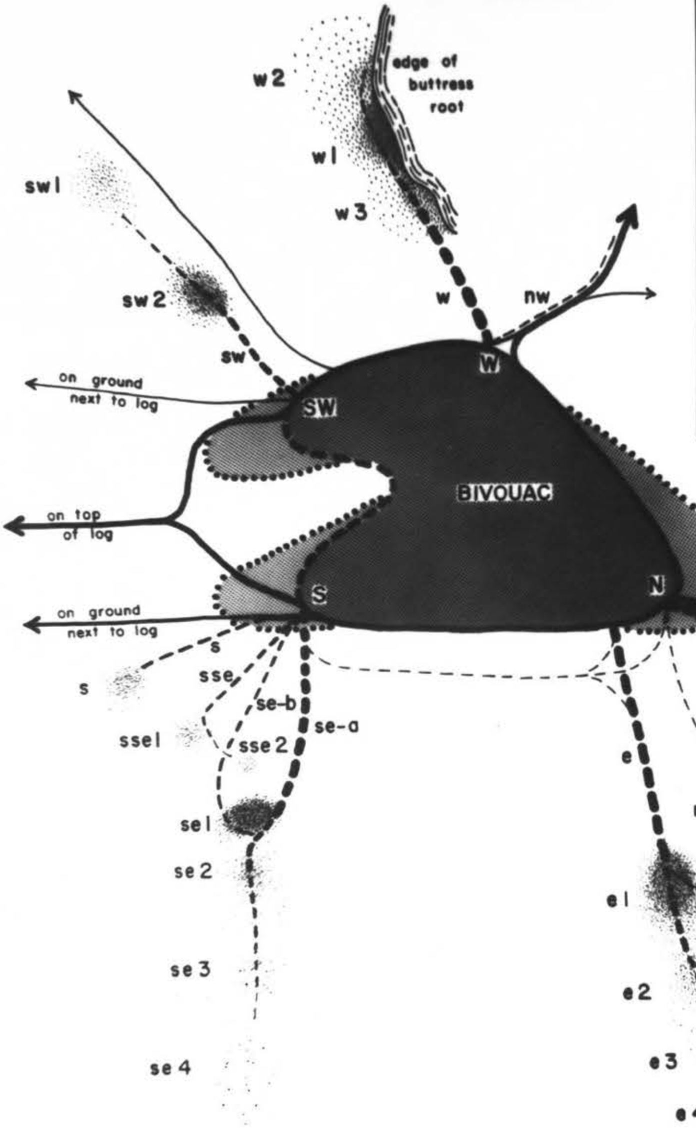
Figure 66. Statary bivouac under large log, the longitudinal edges of which extended slightly beyond N-S and W-SW faces of bivouac. Throughout statary period bivouac changed shape repeatedly; outer dotted lines and more lightly stippled areas indicate maximal extent of bivouac. (Colony '55 B-IV, 12 February to 3 March 1955).

Figure 67. Typical pattern of refuse deposits near statary bivouac in tree where ants have access to bivouac on only one side. Based on several colonies.

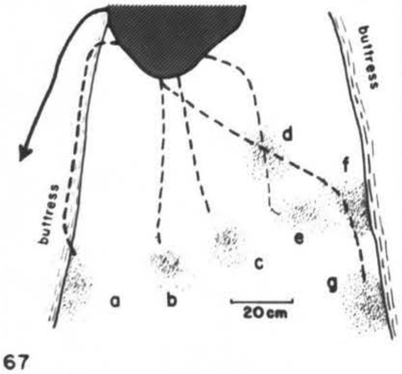
Figure 68. Nomadic bivouac on side of tree, all refuse deposited along edges of large buttresses. (Colony E-107, 19 February 1956).


N
e
edges of liana
ne
root
20 cm

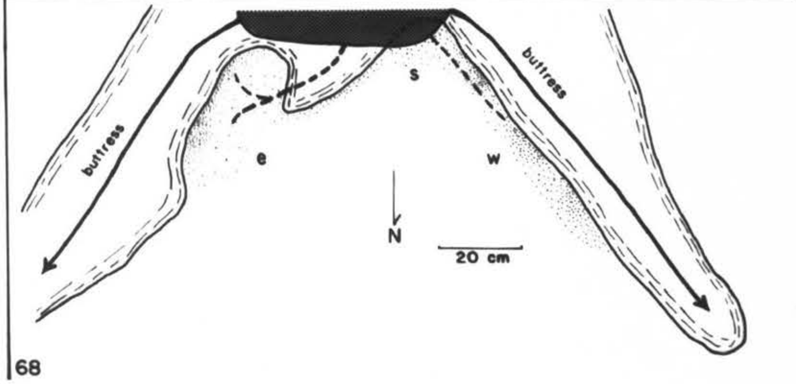
65


w 2
edge of buttress root
w 1
w 3
sw 1
sw 2
sw
w
nw
W
SW
on ground next to log
on top of log
BIVOUAC
S
N
on ground next to log
s
n
s
sse
se-b
se-a
sse 1
sse 2
ne
nne-1
e
n 2
n 1
nne 2
se 1
nne-2
se 2
nne 3
e 1
nne 4
ne
se 3
nne 5
e 2
se 4
e 3
nne 1
e 4
N
20 cm

66


buttress
d
f
buttress
e
c
a
b
g
20 cm

67


buttress
s
buttress
e
w
N
20 cm

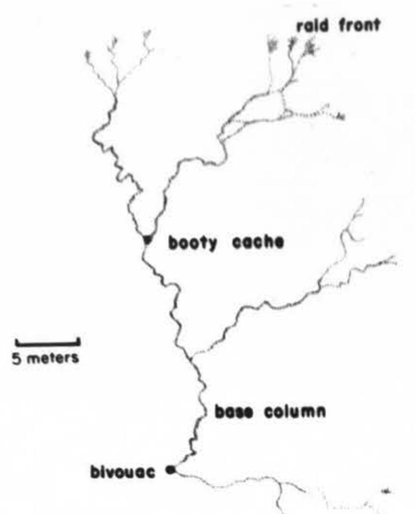
68

Figure 69. Column raid of Eciton hamatum. Advancing front of raid is made up of columns or small groups of workers. Almost all army ants have similar, but usually smaller, "column raids". Prey often is deposited in booty caches at junctions of columns. Base columns extend from bivouac to first forks.

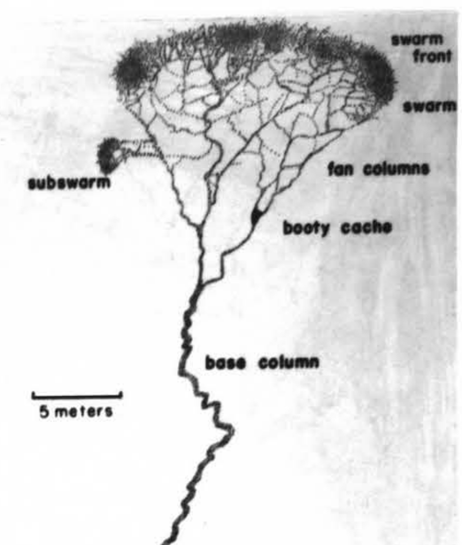
Figure 70. Swarm raid of E. burchelli. Advancing front is made up of large mass or swarm of workers. Anastomosing columns in fan area converge to base column.

Figure 71. Path of swarm raid of Labidus praedator, colony E-230, from 9:55 to 11:10 a. m., 31 July 1956. Swarm raid at any time was similar in shape, but much smaller than in figure 70. Each solid arrow indicates direction and time for majority of advancing ants. Dotted lines show maximal extent of swarm fronts. Dashed line labelled Raid Column is major route along which ants carried booty into a depression. (Bivouac site unknown, not in brush heap or depression.) Parallel lines indicate Fairchild Trail from station 3.0 to about 3.1. Dashed line on left shows edges of large brush heap in which raid could not be followed. All trees are indicated which were close to edges of raid and may have influenced its spread; other trees in main body of raid or farther outside not indicated. Area sloped downhill toward left.

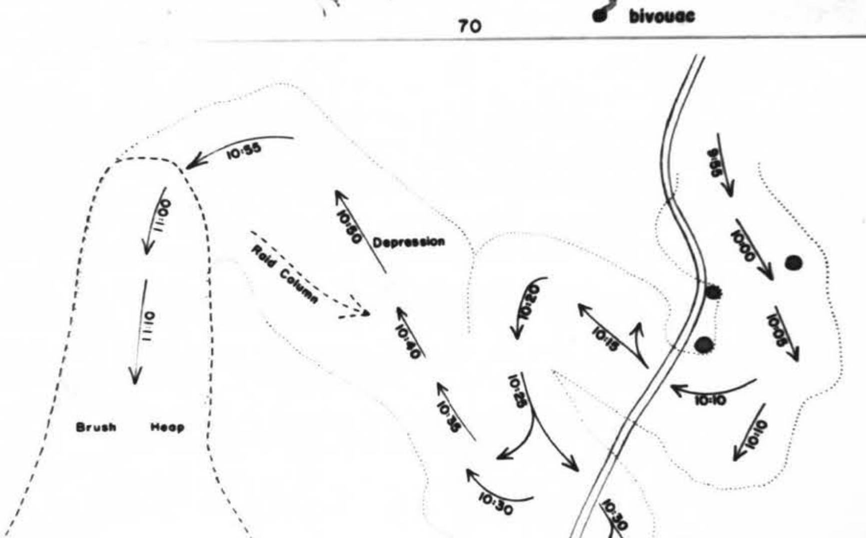
Figure 72. Path of swarm raid of L. praedator, colony E-220, from 10:00 a. m., to 12:30 p. m., 25 July 1956. Ants carried booty primarily along four columns to holes labelled A, B, C and D at times indicated. Parallel lines show Barbour Trail between station 5.1 and 5.2. Area almost level.


raid front
booty cache
5 meters
base column
bivouac

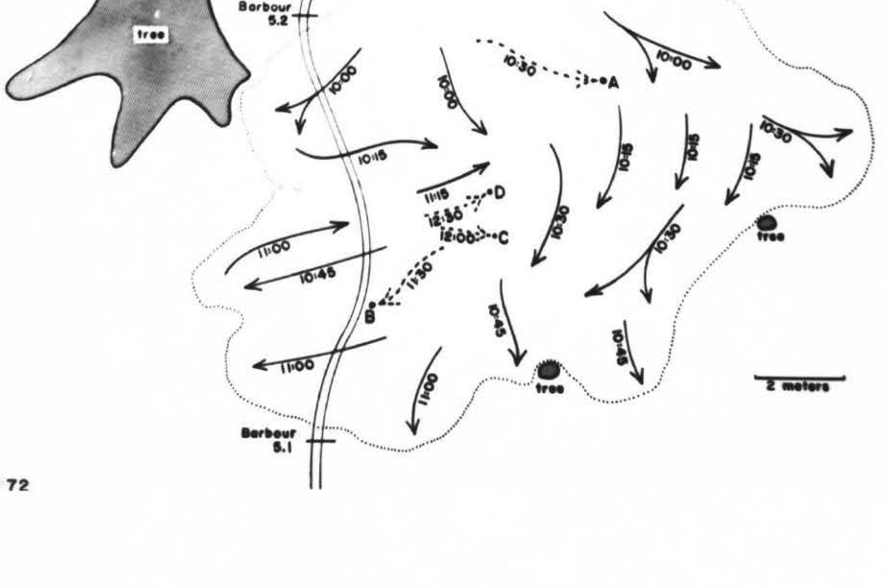
69


swarm front
swarm
subswarm
fan columns
booty cache
base column
5 meters
bivouac

70


10:55
11:00
11:10
Brush Heap
Raid Column
10:50
Depression
10:40
10:35
10:30
10:25
10:20
10:15
9:55
10:00
10:05
10:10
10:10
10:30
trees
1 meter
3 Fairchild

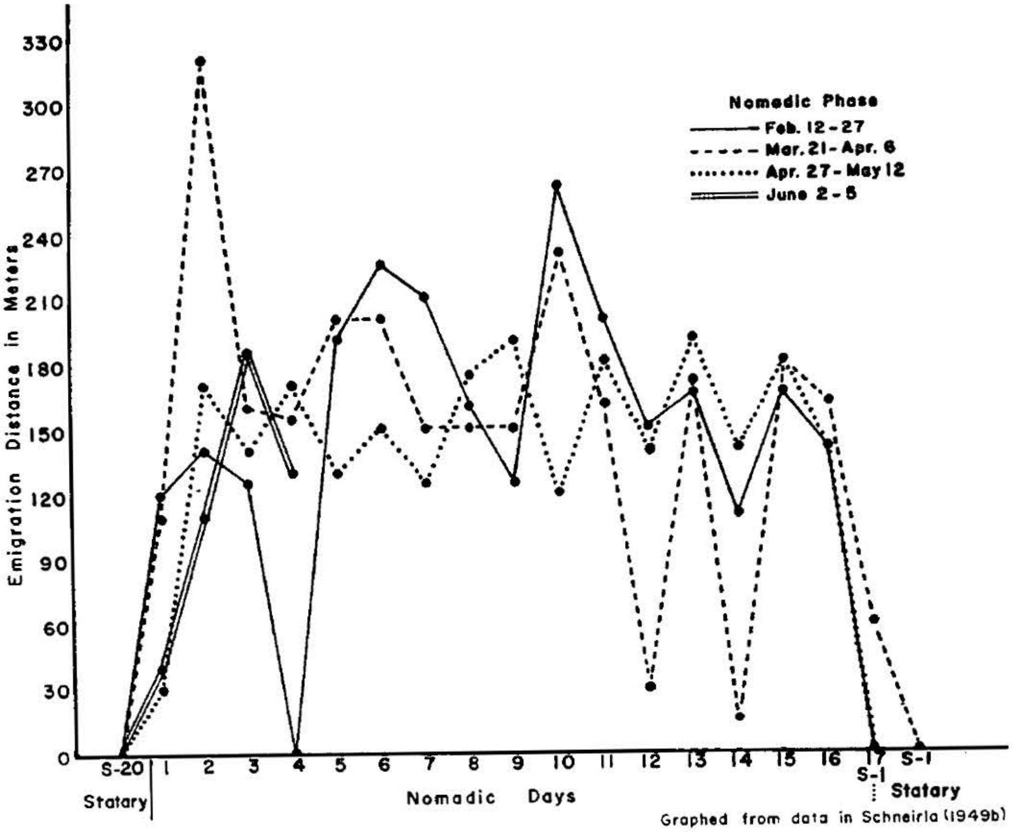
71


?
?
Barbour 5.2
tree
10:00
10:00
10:30
A
10:00
10:15
10:15
10:15
10:15
10:30
11:15
D
12:30
12:00
C
11:00
10:45
11:30
B
10:30
10:30
tree
10:45
10:45
11:00
11:00
tree
2 meters
Barbour 5.1

72

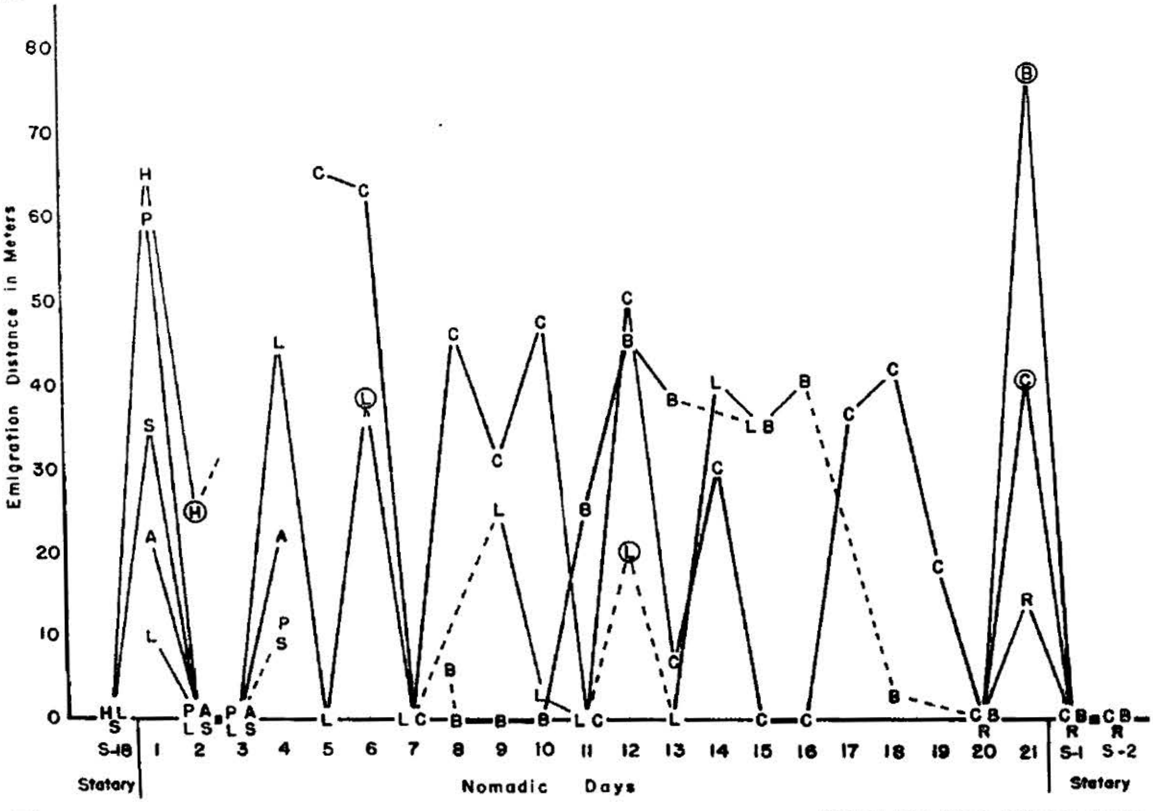
Figure 73. Graph of emigration distances of colony '46 H-B, *Eciton hamatum*, throughout three complete nomadic phases and part of fourth. Distances determined by Schneirla (1949b: 17, 20-22) on Barro Colorado Island.

Figure 74. Graph of emigration distances for eight colonies of *Neivamyrmex nigrescens* in Arizona. Data published by Schneirla (1958). Colonies indicated by following symbols: A = Laboratory-A, B = Bridge, C = Creek, H = Skunk Hollow, L = Laboratory-B, P = Pugsley, R = Rock, S = Stone. Circled letters indicate colony completed its emigration of that distance on following night. Dashed lines indicate distance was not known or not published. Exact day in nomadic phase not known in most cases, but estimated from most complete records.



Graphed from data in Schneirla (1949b)

73



Graphed from data in Schneirla (1958)

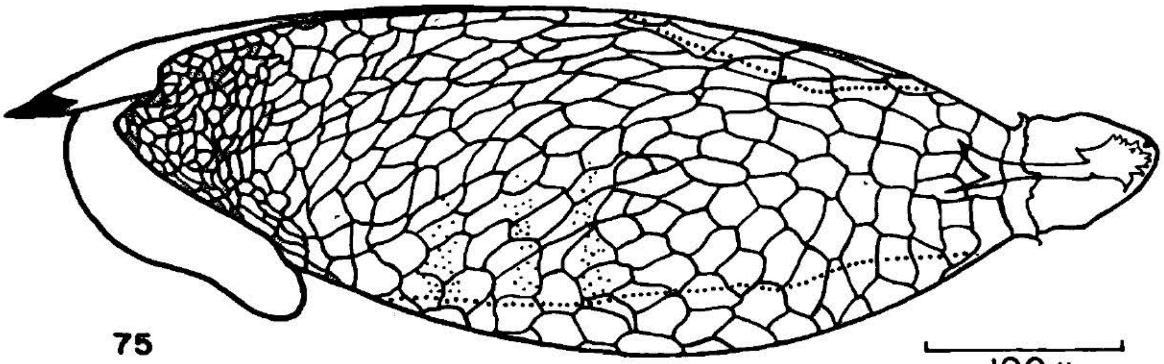
74

Figures 75 to 77. Egg of Stylogaster currani Aldrich with larva protruding from blunt end; egg found on base of wing of Calodexia venteris Curran female (2341-C).

Figure 75. Entire egg with anterior end of larva protruding; three ventral bands of small spines and part of larval body wall can be seen within chorion.

Figure 76. Large spine at posterior end of egg showing one large, dark recurrent spine near tip and one smaller recurrent spine near base of large spine.

Figure 77. Buccal armature and anterior end of larva; small structure anterodorsal to oral hooks is probably antenna; (only right half of larva illustrated).



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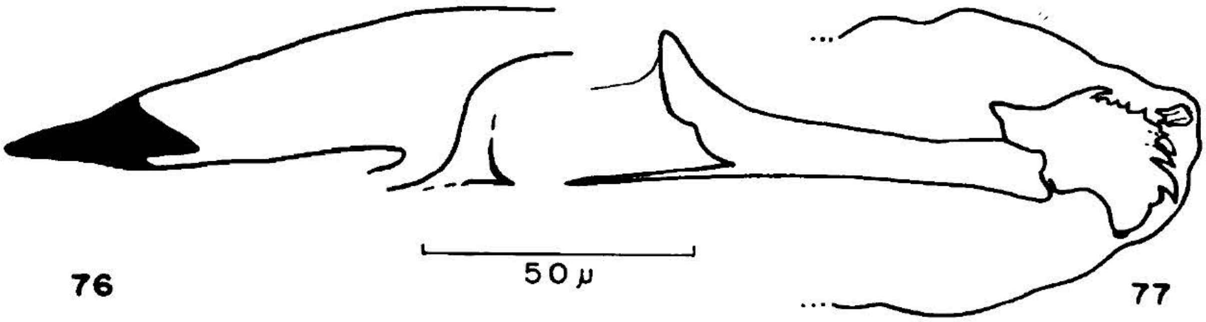

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