# The biology of the fungus-growing ants. Part VII. The Barro Colorado Island, Canal Zone, species

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(With 14 plates)

Barro Colorado Island is situated in the Panama Canal and represents high land (maximum elevation 537 feet above sea level) not flooded in the formation of Gatun Lake through which the Canal passes. It is consequently an artificial island and has no insular characteristics so far as the ant fauna is concerned. Barro Colorado Island is covered almost completely by luxuriant Central American rain forest and has an annual rainfall of about 110 inches. Though having an area of but approximately six square miles the ant fauna is exceedingly rich. It has very likely as many species of ants as any region of similar area in the world. Thanks largely to the foresight and initiative of Thomas Barbour and James Zetek, and the men they have interested, it is to be kept as nearly as possible in a primitive state.

Probably more biological research has been and is being conducted on this island than at any other place in the Tropics of either hemisphere. Eventually it will be possible to give a complete picture of tropical life from these investigations. The following study, based upon very brief and hurried personal observations, is the first to be made here upon fungus-growing ants as a group. More complete studies are much to be desired in view of the general scientific and economic importance of these animals which live in an unusual symbiosis with primitive plants.

Barro Colorado Island is well provided with Attini. Dr. W. M. Wheeler, who spent the summer of 1924 on the island, recognized (1925) 14 species of 7 genera though without identifying more than a new species of Sericomyrmex (S. amabalis). Later he identified Atta cephalotes polita (Lutz, 1929) and Acromyrmex octospinosus echination (Wheeler, 1937). During several weeks in June and a few days in August 1938 I was able to make hasty observations and collections of attine ants on the island. In the collections I have identified 21 species and subspecies of eight genera. For an island of only six square miles, this is a considerable variety which can probably not be surpassed anywhere in a

similar area of rain forest. Twelve species and subspecies are new to science, including two which I described from Dr. Wheeler's collection (1938b). Since many attines are local and rare it is probable that these are by no means all to be found on the island. By comparison, the 1,750 square mile island of Trinidad, B.W.I. contains 27 species and subspecies of 9 genera, the single genus not found on Barro Colorado being Mycetophylax which, in the Caribbean, seems to live exclusively on the seashore and would therefore not be expected on Barro Colorado. On the largest island in the Neotropical Region, Cuba, only five species, each of a different genus, are known. I have recorded (1938b) 49 species and subspecies of 10 genera and subgenera from Bolivia, the largest number from any country so far published, though Brazil, because of its tremendous area and varied habitats, should have more.

The variety of attines found on Barro Colorado would be still larger if it were not covered uniformly by rain forest. The small clearing below the laboratory does not present true savannah conditions so far as attines are concerned. On the grassy Plaza de Lesseps in Panama City, for instance, is found Atta sexdens, a species not found on the island, and the subgenus Moellerius of Acromyrmex comprises another savannah group of species.

On the other hand, Atta columbica tonsipes and A. cephalotes isthmicola which are found in the rain forest of the island, are also found in savannah regions, the former in the west savannah near Juan Diaz, Republic of Panama, and the latter, or a closely related form, on the open slopes of the Cordillera Central of Colombia (Medellín, 5800 ft.; Rio Porce, 3250-3500 ft.).

The majority of the species on the island, however, are probably strictly rain forest species. The species of Apterostigma, for instance, require a habitat which has a uniformly high humidity since their nests are usually in places which could quickly dry out and the fungus grown by them is very delicate. Those species of Trachymyrmex, Sericomyrmex, Myrmicocrypta and Mycocepurus which are found on Barro Colorado doubtless require similar conditions of consistently high humidity though unfortunately only two of the species have so far been reported elsewhere. It is quite possible that some of the soil-inhabiting species may be more adaptable.

An example is *Trachymyrmex urichi* which in Trinidad nests not only in the rain forests of the northern Range and the Nariva Swamp but also on the Piarco Savannah of that island and the llanos north of Cuidad Bolivar in Venezuela. In such adaptability it resembles *Cyphomyrmex rimosus*, *Acromyrmex* and the Attas above mentioned. The new *Cyphomyrmex acutus* is undoubtedly a strictly rain forest species.

The affinities of the attine fauna seem to be largely Central American as would be expected though the distribution of a very few attines is even imperfectly known, the majority of species being recorded from the original single collections. Cyphomyrmex costatus and Myrmicocrypta ednaella, hitherto known only from Honduras, are represented on Barro Colorado. Apterostigma collare, A. dubium, and A. angulatum are common to Costa Rica and the island. On the other hand, the above mentioned species of Atta, Cyphomyrmex rimosus and Apterostigma mayri are common to both Central and Northern South America. Cyphomyrmex costatus has as its congener in neighboring Colombia (Rio Porce) a closely related new species, C. colombianus (Weber, 1940).

The typical situation for an attine nest is in the soil in shade. The smaller species habitually nest in one or more cells, the upper cell occasionally being against a partially imbedded stone or piece of wood, but in most species it is a few centimeters down in the soil. Some species suspend the fungus garden from the ceiling of stone, wood or soil; others use roots penetrating the cell for a support for the fragile garden. Nests of attines on Barro Colorado are noticeably more abundant on the clay ridges radiating down from the highest point of the island. The soil drains freely down the slopes and the forest is not so dense as to drive out the animals and plants upon which the attines directly or indirectly depend. In the densest tropical forests life is appreciably scarcer than in forests with moderate light. The ants of the species Cyphomyrmex rimosus and its numerous subspecies are about two millimeters in length and the colonies consist usually of about a hundred adults. These small ants frequently nest in humus about the roots of epiphytes or under the bark of living or dead trees, sometimes several feet from the ground. The highest nest found seems to be one at an elevation of 92 feet on a Cassia tree which was itself 180 feet tall that I examined in British Guiana. The larger ants of the genus Apterostigma form smaller colonies and these may be found among humus or in decayed wood several feet above ground. The Myrmicocrypta and Mycocepurus on the island are terrestrial though a single species of Myrmicocrypta, M. spinosa (Weber, 1937, p. 383) has been found in a tree several feet above ground.

The external indication of the nest of the small species, except those of Cyphomyrmex, is usually a small crater several centimeters in diameter. The crater is often erected in the form of a friable turret in Myrmicocrypta, Mycocepurus, and Trachymyrmex but this is easily demolished by a shower. A short tunnel leads to a cell whose size varies with the species, an average being the size of an orange. In some species a second cell may be beneath the first and there may be still others. The commonest attine, Cyphomyrmex rimosus, produces no external indication to the nest and appears to occupy previously existing cavities in the soil or wood. A frequent situation for rimosus is inside a curled-up decayed leaf buried in the debris of the forest floor and I found one nest in a dead snail shell on the forest floor in Cuba. The crater formed by colonies of the larger Trachymyrmex species and by Sericomyrmex amabilis is in the neighborhood of ten centimeters in diameter though often washed away by rains. The colonies of the two species of Atta on the island form the conspicuous multiple crater nests, the largest found (R. C. Shannon trail just beyond no. 11 post) (Plate 14) having an uphill diameter of 10.5 meters and a lateral diameter of six meters. Numerous cells 15-25 cm. in diameter and at different levels extend over a large area beneath the craters. The Attas have broad, well-cleaned highways extending sometimes hundreds of feet through the forest to favored plants.

The fungus garden in all species except Cyphomyrmex rimosus is composed of pellets of substrate loosely held together by hyphae and is friable and spongy, with a volume only slightly less than that of the chamber in which it is formed. The fungus consists only of the hyphae in mycelial masses together with special hyphal aggregations known as bromatia. Fruiting stages and spores have never been recorded except in a few cases (Weber 1939a).

Cyphomyrmex rimosus and its numerous subspecies develop a unique fungus garden of cheese-like masses, also

called bromatia, a fraction of a millimeter in diameter, upon insect feces, frequently caterpillar. The bromatia are grayish or amber in color and grow directly from the moist substrate. In feeding, the ants pick up such a bromatium with their mandibles and rotate it between the mouth parts with the aid of the fore feet. As it is rotated the tongue abrades the mass and the juices are absorbed. A bromatium not completely eaten at one meal is re-imbedded in the substrate and grows back to normal size. A bromatium frequently is eaten in situ. New bromatia appear to form by budding off from larger ones. Because of the treatment given the bromatia no conspicuous mycelial growth forms on the substrate. Larvae and pupae, however, are frequently covered with the mycelium from time to time. Brood is kept away from the fungus garden in a separate cell or part of the same chamber.

In the Apterostigma colony the fungus is grown upon wood-boring beetle feces, other insect feces, and upon slivers of decayed wood and other vegetal debris. The fungus grows over the loose mass of such substrate and, if the nest is suspended, the addition of new substrate usually results in the formation of loose, stringy masses held together by the mycelium. In several species the peripheral mycelium grows as a silk-like envelope about the entire mass. Feeding is essentially as described above. In the loose cells of the substrate, the brood is reared.

The fungus garden of all other attines on the island is remarkably uniform considering the variation in size, structure and nesting habits of the ants. The garden is grayish on the outside due to the appearance of the mycelium against the discolored substrate. Inside, the garden is buff, light brown, or grayish-brown in color and is mostly substrate with a scanty mycelial growth covering the pellets and lining the irregular cells or cavities when these are present. In the smallest nests, those of Cyphomyrmex costatus, the fungus garden is quite uniformly grayish and much drier than the moist gardens of most of the other species. Bromatia stud the outside and also the lining of the cells. These are the food of the ants and the manner of feeding is similar to that in Cyphomyrmex rimosus, the ants manipulating the bromatium between the mouthparts and legs and abrading the surface so that the juices may be absorbed. The substrate in the smaller species is a miscellany of vegetal origin, slivers of wood, pieces of decomposing wood, fresh-flower sections, insect feces and even insect skeletons. The latter must be used only as a framework. These particles are manured with the ant's liquid excrement, the latter probably contributing an important part of the proteins and other foods necessary to the metabolism of the fungus. The workers of Atta and Acromyrmex are the leaf-cutters of the tribe and it is this activity which is of importance to agriculture since economically important plants such as citrus and cassava are often stripped of leaves by the ants. They are also a nuisance to gardens, since they readily take the leaves and flowers of exotic plants in general. The leaf sections are broken up into smaller pieces which are bitten repeatedly so as to be reduced to a pulpy mass and are then manured before being imbedded in the garden. As in Apterostigma, the brood is kept in the loose cells of the garden, the larvae and pupae frequently being covered with a mycelium.

Fungus-growing ants are often nocturnal as well as diurnal in their activities outside the nest. The large Attas may cut leaves and excavate during much of the night. The workers of smaller genera are occasionally seen slowly foraging at night for substrate or bringing up soil particles as they enlarge the nest.

An unexpected and unrecorded habit of an attine, Trachymyrmex isthmicus, was observed during my visit to the island. A colony of this species moved their fungus garden and brood, piece by piece, from one site, evidently flooded by torrential rains, to a higher site 52 cm. away on the slope of a clay ridge. The house-and-family-moving started on a rainless, sunshiny day after a week of rain and was finished two days later. Slightly over two loads per minute were taken from the old site to the new. Probably about ten thousand trips were necessary.

Barro Colorado is the home of the guest ant, Megalomyrmex symmetochus, living in the nest of Sericomyrmex amabalis which was discovered by Dr. W. M. Wheeler in 1924. In addition to rediscovering this association I was fortunate in finding another guest ant, a new species of Megalomyrmex (M. wheeleri) living with an entirely different fungus-grower, Cyphomyrmex costatus. Each guest ant develops colonies which live in the fungus-garden of the host or in a small chamber beside it. The guest feeds upon

the fungus grown by the host. Not only is there complete toleration beween the two species but on occasion a worker of one will clean the brood of the other by meticulous licking, as is customary among ants. These are the only guest ants of attines known.

#### II. Observations on individual species

Cyphomyrmex rimosus Spinola (Plate 1)

This species stands at the bottom of the long series of fungus-growing ants. If the Attini are derived from the Dacetonini, as has been accepted by Forel, Emery and Wheeler, this species above all resembles the average species of the parent tribe. In numbers of individuals in the colony, in nesting sites in humus, soil or decayed wood, in slowmoving habit, becoming motionless at the least disturbance, it is a typical dacetonine. Other attine species of several genera are similar in these characteristics but this species is distinct in possessing the squamate hairs and feeble or no spinosity of many Dacetonini, especially Strumigenys and Rhopalothrix, the latter having especially similar compact habitus and mandibles. Yet in the dacetonine Orectognathus antennatus F. Smith of New Zealand, and related species, of a genus not known from the New World, the arrangement of thoracic and petiolar ridges and tubercles resembles closely the arrangement of ridges and spines in Mycocepurus smithi Forel. It is therefore possible that the fungus-growing habit has been acquired independently by these and perhaps other attine genera.

C. rimosus is the most widely distributed of all attine species, having almost exactly the range of the entire tribe but not recorded quite as far north in the United States, evidently being confined for the most part to the Gulf of Mexico coast.

The species is highly variable and a number of subspecies and varieties have been described. Some will probably prove on detailed study to be not valid. Such a form may be *C. rimosus* var. *major* Forel, of which Forel (1912, p. 188) writes, in identifying workers from Sorocaba, Prov. São Paulo, Brazil, as this form: «Le type de la variétté est de Guatémala, mais identique». All forms have probably similar habits

though nothing is known regarding the habits of most of them.

C. rimosus and its numerous forms are unique among Attini in that they grow a fungus lacking hyphae and in the form of small, irregularly polygonal masses, «bromatia», of about a half-millimeter in diameter. The substrate is usually caterpillar or beetle feces. The color of the bromatia varies from dirty gray to a rich, though pale, brown. Wheeler (1907, p. 772) has named this fungus Tyridiomyces

formicarum.

Pará, Brazil, is the type locality of rimosus and the species was described by Spinola in 1851. According to Wheeler (1907, p. 719) the typical form «appears to be confined to northern South America and the adjacent mainland of Central America and Mexico.» The variety minutus Mayr, described in 1862 from Cuba, was believed to be «confined to the West Indies and adjacent shores of North and South America» (loc. cit., p. 722). The ranges, therefore, are confusingly similar and while both were supposed to occur in the Americas, only minutus was supposed to occur in the West Indies. Forel also recorded only minutus from the West Indies. I have, however, collected in Cuba, Nevis, Dominica, Martinique, St. Vincent, St. Lucia, Haiti and Trinidad upon various occasions, ants identical with the common mainland form. The name minutus would lead one to believe that the so-called West Indian form would be smaller. Actually, the size given by Mayr for the type specimen is 2.5 mm., that of a large form, while the typical rimosus was recorded by Spinola as only 2 mm. long. My West Indian specimens agree with Mayr's in size.

From the above considerations it seems probable that minutus is a synonym and I am so considering it. It is possible, of course, that the typical rimosus has not been correctly identified and is an unrecognized small form, in which case minutus would become the most widespread and common form of the species.

Cyphomyrmex rimosus is distributed generally over Barro Colorado and is to be found under logs and stones, between decayed leaves and in similar places which maintain a uniformly high humidity and fairly constant temperature. Such conditions may be met in trees. Near the Mazaruni River, British Guiana, I found a flourishing colony in the tangled

mass of roots and humus at the base of a giant aroid at an elevation of 92 feet on a 180-foot Cassia tree. On the xero-phytic island of Patos, between Trinidad and Venezuela, other colonies weere found nesting in the humus lodged at the bases of six-foot tall bromeliads growing from the ground. In the latter instance the nests were kept moist by frequent clouds passing over the xerophytic forest. In similar situations on Barro Colorado this species undoubtedly will be found.

A nest of this species, under a small flattened stone  $(23 \times 12 \times 12 \text{ mm.})$ , occurred close to a nest of the new subspecies breviscapus, the latter under a small piece of termite-ridden wood contiguous to the stone under lime trees in the laboratory clearing. Aside from one being under a small stone, the other under a small piece of wood their habitat appeared identical since both were in irregular chambers in reddish clay soil. When the nests were exposed, workers of Ectatomma ruidum Roger and a small black Pheidole invaded them and ran off with brood. Both colonies had brood in one set of galleries and the fungus garden on insect feces in other galleries. As in other nests of rimosus the brood is often kept in the higher galleries next to the covering wood or stone where the temperature may become somewhat higher in mid-day and thus speed the time of development.

The usual nest of *rimosus* and its forms contains several score to around one hundred workers with one or several queens. Wheeler (1907, p. 769) records colonies of *C. rimosus comalensis* Wheeler in Texas «comprising a hundred or more workers and from one to three dealated queens.» From the type nest of *C. rimosus venezuelensis* Weber in Venezuela 175 workers were taken. From the type nest of *C. rimosus curiapensis* Weber, also in Venezuela, 90 workers, 7 males and 5 winged females were taken. Unfortunately lack of time prevented the thorough collecting of each colony from their ramifying chambers in humus and no queens were taken. These subspecies are known only from the original collections. The populations of the colonies of the other forms of *rimosus* are not recorded but are probably similar to those above.

What impressed me at the time as one of the largest colonies I ever saw and one with the largest number of queens was a colony found across the bay from Panama

City, R. P., June 16, 1938, 174 workers and 44 dealate queens were collected, a proportion of only four workers to each queen. If we suppose 10% of the workers and one or two queens to have been overlooked, a likely possibility considering those workers probably foraging, their well-known nearly invisible habitus in nature when disturbed, and the haste with which this colony had to be collected, the numbers would be 191 and 46 respectively, a ratio the same 4:1.

No ant colony known to me from the literature or from personal collecting had any such high proportion of quens to workers. The type colony of *Trachyrmex ruthae* Weber in Trinidad had 280 workers, 23 dealate queens, 7 alate females and 23 males. This colony therefore had a ratio of about 12:1 for workers and queens but probably some of these latter were alate forms which lost their wings shortly after the colony was collected. For a possible explanation of the high proportion, the ecology of the Panama colony may well be considered.

The nest was in a section of a rotted twig 2.5 cm. in diameter and 13 cm. long which was lying on the sandy beach in the shade of bull's horn acacia (A. costaricensis Schenck), mesquite (Prosopis chilensis), manchineel (Hippomane) and other plants just above high tide level. The twig was on the bare sand some centimeters from other debris. Irregular chambers under the papery bark, probably tunneled by woodboring beetles, were occupied by the colony. Brood was keptin some of the chambers, the fungus garden in others. At this time, late, sunny morning, workers were carrying in beetle feces, not caterpillar. It was necessary for them to forage back under the bushes since to the south and west stretched a short beach, then the bay. At this time the rainy season was in full swing and the previous month was one of record rainfall with several rains every day. The prevailing winds would come from the north or east and thus blow from the mainland towards the bay. The colony probably had produced a brood of winged females and males which became adult at the onset of the rainy season. Heavy and continuous rains with winds driving seawards may have prevented some females from leaving the nest, others may have come down from their marriage flight to the barren beach. The result may have been the adoption of some of

these females, fecundated or not, into the colony and the consequent high proportion of females.

Cyphomyrmex rimosus Spinola ssp. breviscapus Weber

This subspecies is readily told in the field from the typical *rimosus* by its paler color and smaller size. Some workers, however, may be almost as dark. Under the microscope the shorter antennal scapes serve to identify it.

It is probably of general distribution on the island. Stray workers were found in debris on top of a large fallen tree as well as under a small rotted log on the ground. One colony was nesting in a knothole in a rotted log on the ground in dense shade on a steep slope. Another, found in a very wet and friable rotted piece of wood on the ground, had the brood distinctly segregated from the fungus garden in small, irregular cells. The fungus garden was developed on insect feces. When the nest was disturbed the workers carried the brood and fungus gardens to other cells already present in the wood.

The nest of this subspecies beside the nest of the typical form in soil as described above indicates further the similarity in ecology.

Cyphomyrmex rimosus Spinola ssp. trinitatis Weber

This subspecies is readily told from the other *Cyphomyrmex* on the island by the well developed spines or tubercles on the thorax and by the sharp ridges of the head.

Specimens from Barro Colorado resemble closely the cotypes of the ssp. trinitatis which I found in 1934 on the summit of El Tucuché (3072 ft.) in the Northern Range of Trinidad, B.W.I. More detailed study taking into account the range in variation may show them to be closely related but different subspecies. The summit of El Tucuché has an annual rainfall comparable to that on Barro Colorado but bathed much oftener in clouds. The type ant colony was found under a piece of wood on the grassy mountain top and the fungus garden was developed on insect feces in customary rimosus manner.

Though found only in the northeastern part, this subspecies is probably generally over the island. The ecology of the ant is evidently similar to that of the other forms of rimosus and nothing peculiar about the fungus garden was observed.

All three nests found were in dense shade on steep slopes. One nest was in a cavity in the soil under a rock. The brood was separate from the fungus garden, the latter being developed on insect feces. Another nest was between two dead leaves under a piece of decayed wood on the ground close to an Apterostigma angulatum colony with four fungus gardens. The third nest was in reddish clay and humus under a piece of decayed wood.

### Cyphomyrmex costatus Mann (Plate 2)

This species was described by Dr. W. M. Mann in 1922 «from three workers found in rotten wood» at Lombardia, Honduras. The species has not been recorded elsewhere.

On my first visit to Barro Colorado I found a single nest June 23 and stray workers June 26. On my brief return visit of four days in August I found no less than nine colonies of which four contained a hitherto unknown guest ant. The workers agreed well with Dr. Mann's cotypes which I hastily examined in December 1938 at the U.S. National Museum. The cotypes, however, are slightly smaller, paler and perhaps less sharply sculptured, though this may be an optical effect caused by the paler color. When the female and male of the Honduran costatus and the male of the Panama ants are found, it may be necessary to separate them as two forms. The June nest was on a well-drained ridge in somewhat open forest and was under a small stone  $6 \times 20$  cm. in diameter by 4-8 cm. thick. The single fungus garden filled a small cell 15×10 cm. in diameter and was suspended on rootlets. The fungus garden resembled that of the higher attines and was unlike that of rimosus, being composed of small pellets of vegetal debris covered with a mycelium containing loose bromatia. In the soil about the nest were a dealate female Strumigenys (S.) and two small worker ponerines. The colony consisted of 24 workers and a single queen with a small amount of brood. Only worker pupae were in the nest and these were enclosed in cocoons in which were imbedded tiny particles of debris, evidently acquired in the spinning. The larvae were less plump than those of Apterostigma immobile, e. g., but had a similar disposition of hairs. These were confined to the head and ventral part of the thoracic region and were simple, curved and almost transparent. Those of the thoracic region differed from similar hairs of the *Apterostigma* in being irregularly curved at the distal half. One larva was  $0.74 \times 0.50$  mm., viewed laterally, the head being curved toward the posterior tip, another was 1.26 mm. long and 0.51 mm. thick medially.

The larvae are easily distinguished from those of Maga-lomyrmex wheeleri, the latter having the body segments indicated by distinct constrictions instead of being smoothly joined as in Attini. The pilosity of the Megalomyrmex, though moderately scant, covers the body uniformly, the hairs being upright and apparently sometimes truncate, sometimes divided apically. Mature larvae are also larger, one being 1.56 mm. long.

One of the June 26 stray workers was driven out from under a fallen leaf by an army of *Eciton (Labidus)* sp., the other was among debris on forest floor.

Two of the nine colonies found August 13 to 16 contained colonies of the new guest ant, which I have named Megalomymex (Cepobroticus) wheeleri, (Weber, 1940a), and two contained single females of the guest ant. Unfortunately time prevented only the briefest of notes on the relationships but they show that the guest ant lives on the fungus grown by the host as M. (Cepobroticus) symmetochus Wheeler lives on the fungus grown by Sericomyrmex amabilis. One nest of mixed colonies and one nest of costatus with the female guest ant were taken alive on the Norwegian oilburning freighter which I took to San Francisco, California. The irregular temperatures, numerous handlings and vibration of the ship ruined their fungus gardens and few observations could be made before the colonies died.

The finding of nine colonies in a brief period in August compared with the finding of a single colony over a much longer period in June perhaps indicates a seasonal periodicity. Both periods were in the rainy season, however, and the evidence is hardly more than suggestive. I noticed a similar apparent periodicity in *Mycocepurus smithi trinidadensis* Weber in Trinidad. The tiny craters of this ant were much less often seen in the full rainy season than towards the end and in the dry season. During rains the craters, of course, would be washed away but it would be interesting to determine whether there was a tendency to suspend activity, above ground at least, during the rainy season.

All August colonies of costatus were in small earth cells

under stones and were partially supported by rootlets. The fungus garden was bluish-gray in color and friable, crumbling easily. Two colonies, evidently mature, had ellipitical fungus gardens  $32 \times 13$  mm. and  $30 \times 20$  mm. in diameters. respectively, and were about 10 mm. deep. The former contained 59 workers and a single queen and a dealate female Megalomymex. Part of the latter colony was lost in its observation nest on shipboard and the part remaining consisted of 31 workers and eight alate and dealate females. The smallest nest found had a tiny fungus garden 8×5 mm. in diameters and contained ten workers and a single queen. This nest was in soil under a crevice between a 13 cm. triangular rock 150 cm. from the 32×13 mm. nest above mentioned. The ants had erected a wall of wet, loosely adhering soil grains around the fungus garden. A peculiarity in all the fungus gardens was the use of chitinous fragments of insects, especially ants, and tiny snails (both helicoid and Planorbis-shaped) as a framework for the garden. Heads of ants of Ectatomma ruidum, Ponera, Anochetus, Odontomachus spp., Labidus or Acamatus, Pseudomyrma, Pheidole spp. Cephalotes, Azteca and Camponotus spp. were easily recognized. The Pseudomyrma, Azteca and Camponotus were arboreal species so that the costatus must have acquired the heads from fallen carcasses. Of particular interest was the finding of the petiole of the fiercely-stinging Paraponera clavata worker in one nest and the head of a worker Acanthoponera, a rare genus, in another. Other recognizable remains were the heads of Nasutitermes soldiers, Hemiptera, and Coleoptera and the spiny cephalothorax of spiders. The nest containing 59 workers costatus had in it a snail, beetle elvtra, the Paraponera petiole and heads of Anochetus, Labidus or Acamatus, Cephalotes and Camponotus spp. Other nests had a similar variety.

### Relationships between the host and guest ants

Of the four costatus colonies containing Megalomymex wheeleri, two contained only single females of the guest ant. One female was in the most populous nest, that found August 15 containing 59 workers and a queen. The guest ant scurried from beside the nest when the stone overlying the nest was removed and no further observations were possible on the relationships. The second guest female was also beside the host nest and it was noted that she was much quicker than the costatus. The colony contained more than 44 workers and nine alate

and dealate females. She was removed with the colony and taken aboard the ship for the journey north. No suitable containers were available and the danger of losing her deterred examination of the box in which the ants were kept very often. August 20, at sea off the Pacific coast of Southern Mexico, she was found to have taken a position on the ceiling of the container close to a cluster consisting of a few costatus workers and winged females, all being above the fungus garden. The whole nest was preserved shortly after, since colder weather and the vibration of the ship were killing the colonies.

A nest of costatus found under a small stone August 13 contained 35 workers and one queen, white in an adjacent cell there were 56 workers and three dealate queens of the Megalomymex. In this case the Megalomyrmex clearly outnumbered the host ants. The whole colony of the guest ant was easily collected, since the ants milled about instead of trying to escape, though they could move rapidly. This cell was less than 10 mm. from the costatus fungus garden yet there was no mingling of the two and no hostility was exhibited between the species.

The second Megalomyrmex colony was found August 15 (Plate 2). The nest was at the very side of a costatus fungus garden 30×20 mm. in diameters and the only opening of the single cell was to the chamber containing the fungus garden. The part of the costatus colony which was eventually preserved consisted of 31 workers and eight dealate and alate females. The original colony was somewhat larger. The part of the Megalomyrmex colony which was eventually preserved contained one worker and one female but was originally larger. These ants were sluggish and easily captured. The two colonies were gathered up into the same container. Three hours later, when it was opened, two Megalomyrmex workers were seen beside the newly built-up fungus garden. Several guest workers gathered what seemed to be their larvae and ran with them over the fungus garden. The costatus ignored them. The guest ants made no effort to take refuge in the soil farther away from the garden where there were suitable crevices. This mixed colony was also taken on board ship, but no significant observations could be made before it was ended.

## Cyphomyrmex acutus Weber

This new species is readily distinguished from the other *Cyphomyrmex* on the island by its spinose occipital corners, acute, paired carinae of the vertex and convex thorax bearing short spines.

Only two workers were found, one June 28, the other August 13, and the species is probably rare and local in distribution. The first worker was walking over a wet, prostrate, dead tree trunk across the Zetek trail at about No. 10. The second was found near the beginning of R. C. Shannon trail and was carrying substrate along a fallen tree. Unfortunately

when the ant was picked up the substrate was dropped and lost.

The species will probably be found to grow a fluffy mycelium on vegetal substrate as does *C. bigibbosus* rather than the cheese-like bromatia without hyphae of *C. rimosus*.

Mycocepurus tardus Weber (Plate 3)

Ants of the genus *Mycocepurus* were not found by Dr. Wheeler on his visit in 1924 but he surmised that they might occur. They are rare, inconspicuous ants and very easily overlooked. During my hasty investigations of the attine fauna I found workers of this genus upon several occasions but unfortunately time was lacking for detailed study. They proved to belong to a new species differing from the widespread *M. smithi* and its forms in details of spinosity and color. *M. smithi* occurs in Mexico, Cuba, several of the Lesser Antilles and Trinidad. I found *smithi* nesting in the grounds of the Gatun railroad station in the Canal Zone only a few miles from Barro Colorado, yet found only the new species on the island. Either may be readily separated from other attines likely to occur on Barro Colorado by its tiny size (1.6-2.0 mm.) and thorax covered with high, sharp spines.

M. tardus is slow-moving and blends in so well with the clay on which it is found as to be seen with difficulty. Near the top of the island (Wheeler 12) at an elevation of fully 500 feet a crater of clay pellets made by the ants was found. Another crater at Snyder-Molino 2 was in the form of a simple, irregular cone of fine clay pellets 23 mm. high and 26 mm. in basal diameter.

The two days preceding were rainless, otherwise such a cone would have been readily washed away. This species probably resembles *M. smithi* in forming a small cell several centimeters in diameter containing a grayish fungus-garden.

## Myrmicocrypta ednaella Mann (Plates 4, 5)

This species was described by Dr. W. M. Mann from specimens taken from colonies beneath stones at Lombardia, Honduras. Dr. Mann (1922, p. 48) found that «the fungus gardens are pendulous, hanging from the underside of the stones into little pockets, which evidently are excavated by the ants. They are small in size — a little smaller and somewhat the same shape as a thimble. There are few individuals in a colony.»

My specimens from Barro Colorado resemble the type specimens closely but there are small differences which, if constant, may necessitate the separation of these ants as a new form. The species is widely distributed over the island but inconspicuous. It nests in the soil, especially on the clay ridges of the island.

Entrance to the nest is in the form of a crater of irregular shape which is readily washed away by rains. In the latter case the nest opens by a simple hole which is very readily overlooked. The crater may be in the form of a friable turret, one such turret being 35 mm. high and 40 mm. wide at the base. One nest had several external openings and a multiple crater of fine, red clay pellets. The craters were in the form of ridges which paralleled and did not separate the openings from one another. Another nest, found on the last of three rainless days, had a single opening which was half-surrounded by a ridge of clay pellets 31 mm. high and 97 mm. in length. Several craters were found in the form of irregular piles of clay pellets 10 to 20 mm. high and about 30 mm. in diameter.

The cell and fungus garden constructed by this species are large compared with the size of the ants. The cell of one nest was at a depth of 100 mm, in the soil and was 55 mm, high and  $90 \times 65 \text{ mm}$ , in horizontal diameters, being elliptical in shape with a flattened base. The garden was dull gray on the outside and light brown internally, the outer surface being speckled with bromatia. It was more compact and less friable than the garden of such ants as Sericomyrmex amabalis. The substrate contained clorophyll but was otherwise of unrecognizable vegetal origin.

Another nest, which was in humus under a breadfruit tree beside a stream, had a cell 50 mm. high and  $30_i \times 80$  mm. in horizontal diameters. The fungus-garden was similar to that described above and likewise was developed on chlorophyll-rich substrate. Within several centimeters of the nest were nests of Ectatomma ruidum Roger, a tiny black Pheidole, and a small Tranopelta. These ants also tolerate other attines, one nest being found 10 cm. from a nest of Trachymyrmex isthmicus and another 40 cm. from a nest of T. cornetzi gatun. This species resembles other attines in moving with great slowness.

## Apterostigma dubium Weber

I described this species (1938b) as a subspecies of A. collare Emery from specimens which Dr. W. M. Wheeler collected on Barro Colorado in 1924. Metatypes were listed from Costa Rica. Two females which I took on the island in 1938 agree closely with the holotype female of dubium and the constancy of their characters together with those of the worker cotypes indicates that dubium is specifically distinct from collare. Numerous workers collected without their queens resemble the cotypes of both dubium and angulatum. They are not separated here. Where queens occur with workers the two species are easily separated on the basis of angular frontal lobes and distinctly carinate gaster in angulatum females compared with evenly convex lobes and feebly carinate gaster in dubium females.

One female was taken June 14 with her fungus garden from a cell beneath a sliver of black bark on the side of a rotted buttress of a giant tree (between Wheeler 8 and Lake trails). Nearby, where the buttress joined the trunk, was a bivouac of Eciton hamatum Fabr. The fungus garden was about 2.4 cm. long and was firmly attached by hyphae at the top of the cell at one side. There was no indication of a mycelial envelope. The fungus garden was a mottled gray in color and the substrate consisted of a variety of small pieces of vegetal debris from yellow to dark brown in color, together with several small insect feces. Only a single egg was found, which was elliptical, 0.31 × 0.43 mm., and white in color.

The second female was taken August 13 in its cell under bark of the Anacardium tree being studied by Doctors Park, Voth, Williams and others. The nest occurred in Quadrat 2 at a height of 167 cm. The fungus garden was 20 mm. high, 8-12 mm. wide and as deep. Over it grew a fluffy hyphal envelope, clearly a natural growth and not made by the sole ant. The hyphae were not interwoven. The substrate resembled closely that of the other female. The garden contained a single white pupa, 3.4 mm. long, whose eyes were just becoming pigmented and whose frontal lobes appeared evenly convex. No larvae were found but two elliptical, white eggs  $0.33 \times 0.43$  mm. were imbedded in the garden.

Apterostigma angulatum Weber (Plates 6-9, 13)

I described this species (1938b) as a new subspecies of A. collare from specimens which Dr. W. M. Wheeler took on Barro Colorado in 1924. Metatypes were listed from Costa Rica. On the basis of numerous collections which I made on the island in 1938, I now regard it as a distinct species because of the constant angular character of the frontal lobes in both the worker and the female together with other characters. In collare the lobes are evenly convex, the neck much narrower, etc.

Apterostigma angulatum and A. mayri appear the commonest species of the genus on the island. The most conspicuous of the two species is angulatum because of its larger size and larger nests. Both, however, in common with the other species are dull brown in color and move so slowly, becoming motionless at the lest disturbance, as to be easily overlooked. The gray fungus gardens are more readily seen when rotted logs are broken up or overturned. I have found the nests in all parts of the island from near lake level to the top at Wheeler 15. This species nests both in the ground and in rotted wood. While the species of this genus are comparatively little known, none has been recorded to be polydomous, i. e, having a number of fungus gardens in separate cells as in higher attines. I found, however, several colonies of angulatum on the island nesting in this manner and also a species near mayri in the Andes (5800 ft.) above Medellin, Colombia, with a nest of three distinct and separate fungus gardens.

The largest number of fungus gardens found was seven in a prostrate, wet, rotted log 240 cm. long and 16 cm. in diameter, on the top of the island June 30. The fungus gardens extended over 115 cm. Each was several centimeters in diameter, grayish in color, and developed on small particles of vegetal debris and wood-boring insect feces. All were collected and the ants and brood contained in them examined with the following results. Eggs and non-adult larvae were not counted.

In this colony 133 workers, 21 winged females and one queen therefore were recovered. It is quite possible that a few workers were not in the nest, although rains a few hours before and an approaching rain which fell as I was examining the colony probably meant that few, if any, were

	Large larvae	Pupae	Workers	Wingedfemales	Queens
Garden A	$\overline{2}$	3 female	25	2	one
Garden B		2 worker	29	2	
Garden C	3	1 worker	2	3	
Garden D	<b>2</b>	1 female	25	1	
Garden E	1	2 worker	3	1	mpilita managina
Garden F	2	6 *	34	10	
Garden G	2	2 worker	15	2	

out foraging. A small male mosquito was collected with one garden and a non-ant insect larva and pupal case were collected with another. A colony of a small ponerine ant also nested in the log and these workers were collected about several gardens.

A polydomous nest found June 18 on a steep slope was in a crevice in red clay soil (Plate 6). A large angular rock evidently had rolled down the slope, leaving the crevice exposed which had extended against the side of the rock embedded in the soil. The crevice was exposed on the east side. Three fungus gardens in a line show in the photograph and a fourth was present on the left side. All were suspended from the roof and none was enclosed in a compact mycelial envelope but each was loosely and irregularly cellular within a somewhat continuous covering of substrate and mycelium. The middle fungus garden in the photograph was conic in shape, 55 mm. long and 28 mm. in basal diameter. It had a conspicuous opening to the loosely cellular interior. The right-hand fungus garden was collected and had in it fourteen workers. one callow, four larvae of varying size, but no female. Workers wandered back and forth between all four fungus gardens.

The outer covering of each fungus garden was studded with amber fecal droplets 2-3 mm. in diameter. These fecal droplets when excreted were undoubtedly much smaller but had probably absorded moisture from the saturated atmosphere and grown in size.

Near this colony were found on June 24 two other colonies of angulatum, each eight to nine meters away from the one described and from each other. One of the colonies had a single fungus garden on the under surface of a rotted

<sup>\*)</sup> Two were advanced enough to be determined as male and female pupae.

log resting on the steep hillside. The garden was damaged in discovering it and the log replaced. Three days later the ants had rebuilt the garden but the hyphae were growing rather wildly. It was significant that the hyphae showed a tendency to grow in the form of an envelope around the substrate and over the wood. The other colony was nesting between two angular corners of a large rock on the under surface imbedded in the soil. The garden did not have an envelope.

Other nests found in several parts of the island resembled the above nests in being under rocks or wood. The fungus gardens showed a tendency to develop a mycelial envelope. One such nest was under the same rock as that of Acromyrmex octospinosus echinatior and was 46 cm. away. The fungus garden, enclosed completely in a mycelial envelope, was  $35 \times 25$  mm. in diameter and 30 mm. high. It was attached by the envelope as well as the substrate to the flat undersurface of the rock and also to the rock on one side and humus on another.

An unusually symmetrical and compact nest (Plates 7-9) was found June 22 in overturning a rotted log. Firmly attached to the under surface was the single fungus garden 45 mm. in maximum length, 32 mm. in maximum width and 17 mm. in maximum height. It was surrounded entirely by a silk-like mycelial envelope which had on the lower surface three circular perforations, three to four millimeters in diameter for the egress and ingress of the ants. Studding the outer surface of the envelope were many fine bromatia. Inside, the garden was loosely cellular and contained the colony, which consisted of a few larvae, three pupae, thirteen workers and a single queen. Several workers were callow. Several workers may have been foraging, but in any event the colony consisted of less than a score of adults.

### Apterostigma tramitis Weber

This new small species was taken August 13 within a few centimeters of nests of Myrmicocrypta ednaella and Trachymyrmex cornetzi gatun. In unearthing the nest of the Trachymyrmex a tiny colony was found consisting of one queen, seventeen workers, two female pupae, eleven worker pupae, and larvae and eggs. It is a small species, 2.8 mm. in length, which resembles A. mayri in general habitus but

may be easily told by its much shorter terminal antennal joint in both worker and female. The fungus garden was developed on small particles of vegetal debris and wood-boring insect feces. There was little chlorophyll.

## Apterostigma immobile Weber

This new species is close of A. wasmanni Forel and auriculatum Wheeler of South America from which it may easily be separated on the basis of the medial, unpaired tooth in the mesoepinotal impression. This is absent in wasmanni and auriculatum. It could readily be separated from A. calverti Wheeler of Costa Rica, which may occur on Barro Colorado, on the basis of the strong gastric carinae. These are absent in calverti. No other Apterostigma on the island has the strongly carinate thorax.

This species is outstanding in several respects. When the colony was discovered June 22, the behaviour of the ants was notable. The ants, both worker and male, when first disturbed, remained completely immobile for a much longer time than in other species. Then, when they abandoned this attitude, they moved quickly for a moment before again becoming immobile. The worker of the average species will remain motionless for a short time when disturbed and then will move slowly.

The single fungus garden also differed from that of the other Apterostigma species on the island. It consisted of coarse vegetal debris and small sections of dried leaves, all containing little or no chlorophyll, together with insect feces. The whole was very loosely held together by a scanty mycelium which exhibited no evidence of a tendency to develop an envelope. The garden was suspended by a sheet of mycelium, as is customary in Apterostigma, to the under surface of a rotted log which contained a foraging army of Eciton (Acamatus) sp. The garden was damaged in discovering it but was probably about  $10\times8\times6$  or 7 cm. It contained 12 males, 20 workers, two sexual pupae and larvae in cocoons.

The larvae were exceedingly inconspicuous since they were encased in a cocoon of finely fibrous substance in which were embedded small particles of substrate and debris. The larva was tightly curled so that the head faced the posterior end of the body and this ventral area was the only area not covered by the cocoon. From it protruded a few long (about

0.18 mm.), curved hairs which were simple, almost transparent and grew from both the head and ventral body surfaces. The rest of the body was hairless and finely ridged like the pressure ridges of the human finger. These larvae were short and thick, elliptical in side view, like the sexual larvae of Atta cephalotes. One larvae, with its cocoon, was  $1.3 \times 1.7$  mm.; another, shelled from its cocoon, was  $1.7 \times 2.6$  mm. in side view.

#### Apterostigma mayri Forel (Plate 2)

This species, originally described from Trinidad, has a wide distribution in South and Central America. It is generally distributed over Barro Colorado though easily overlooked because of its small size, dull gray-brown color and slow-moving habit, becoming temporarily motionless when disturbed.

Several nests were found in cells in the soil beneath rocks. The beginning of a colony was found June 26 in soil 9-11 cm. beneath a nest of Trachymyrmex isthmicus and 3 cm. to one side. A single female had formed in a vertical lensshaped cavity about 25 mm. high and 10 cm. wide a tiny fungus garden suspended on a rootlet. The garden consisted of very small pellets of vegetal debris very loosely held together by hyphae. A nest found August 15 was under an angular stone and was 37 cm. from a nest of Cyphomyrmex costatus, the two colonies occupying identical micro-habitats. The single fungus garden hung freely from the rock into a triangular cavity  $38 \times 50 \times 63$  mm. The cavity seemingly had been made by the ants. No mycelial envelope covered the garden. This consisted of small particles of vegetal debris, some containing chlorophyll, and insect feces. It contained 44 workers and a single queen.

Beside or under an angular stone 15 cm. in diameter were found on August 15 three fungus gardens a few centimeters from one another. One garden, on a 15×7 mm. dead leaf section beside the stone, contained thirteen workers, two worker pupae and several plump larvae; the second, under the stone, contained two workers, twelve unpigmented worker pupae and two plump larvae; the third, also under the stone, contained only four workers. The three gardens evidently were part of a polydomous nest and the queen either escaped into the surrounding humus or was in a fourth garden which was not noticed. A 9-jointed worker of *Rhizomyrma* was

collected with one of the gardens but very probably was not associated with the Apterostigmas. A similar worker of *Rhizo-myrma* was taken nearby on the same day in another *mayri* fungus garden against one sid of a rock half-buried under leaves.

## Sericomyrmex amabalis Wheeler (Fig. 10)

This species was described in 1925 from Barro Colorado and has not since been recorded. Dr. Wheeler discovered living in ten out of twelve colonies of this species a guest ant, also new, which he named Megalomyrmex (Cepobroticus) symmetochus. He found (1925, p. 162) the guest queen with a few of her workers usually took up her station «in one of the crypts of the fungus garden a short distance — half to three-quarters of an inch — from the Sericomyrmex queen. The guest ants kept their brood in small clusters scattered through the garden and each cluster was cared for by a few workers. Although the ants and their brood were thus intermingled, the workers of each species lavished their attention exclusively on their own eggs, larvae and pupae and were never seen even to transport the progency of the other species from one part of the garden to another.» The colonies of the host usually contained between 100 and 200 workers, the largest nest found containing about 300 workers while the colonies of the guest ant comprised about 40 or 50 workers and in no nest as many as 75. The guest ants fed upon the fungus grown by the Sericomyrmex and there was mutual toleration shown between the two species.

I found this species to be generally distributed on the island and was able to examine two nests, one of which contained a colony of the *Megalomyrmex*. The mixed colony was gathered June 25 and placed in a Petri dish for examination until I had to preserve it June 29 before leaving for Colombia. The brief observations which I had time to make confirmed Dr. Wheeler's more extensive observations in every important detail. The other colony, found August 13 in Quadrat 1 at a distance 60 cm. from the base of the Anacardium tree being studied by Doctors Park, Voth and Williams, comprised four fungus gardens, in none of which were *Megalomyrmex*. A third nest was found August 13 at a distance of 50 cm. from the same *Anacardium* tree but in Quadrat 4, on the opposite side and several meters away.

Time did not permit examination of this nest. Also on August 13 a worker was found carrying part of the hull of the fruit of an «Espinosa» tree. A stray worker found June 25 foraging at 9 p. m. proves this Sericomyrmex to be nocturnal, at least on occasion. Dr. Wheeler noted a dealate female Rhizomyrma sp. in soil about an amabalis nest and I found Rhizomyrma workers in the bottom of the nest of Quadrat 1 above mentioned.

The June nest containing the Megalomyrmex was on a clay ridge in high forest. The nest opening was a mere hole among leaves and a trail of clay pellets led away from it. The fungus garden was 65 mm. below the surface and 35 mm. to one side (uphill) of the nest opening. It was 35 mm. high and 60-65 mm. in diameter, being elliptical in form except for the flattened base. The fungus garden was friable, gray externally and light brown internally, and was developed on a vegetal substrate. The ccolony of Megalomyrmex was in the garden near the base. In collecting the nest the colonies were thoroughly mixed with the broken fungus garden but no hostility was shown between the two species. By 1:30 p.m. June 27 the garden had been reconstituted. The queens of the two species were not visible but workers of both were wandering freely about. A Megalomyrmex worker spent fully a minute carefully cleaning itself in a cell containing Sericomyrmex pupae of different ages and host workers without being molested. Three host workers were in another cell licking guest larvae and pupae. The next morning the host ants seemed to have taken possession of one cell in the garden and were concentrated there. At 9:30 p.m. June 28 a Myrmicocrypta ednaella worker was placed in the nest. It quickly ran down into one of the cells of the garden and disappeared. The Sericomyrmex workers were disturbed but did not pursue. Workers of Apterostigma angulatum and A. mayri were also placed in the nest. They ran into the clay surrounding the nest and did not disturb the hosts. At 8 o'clock the next morning none of the alien ants except an Apterostigma mayri could be seen. This was in the clay 15 mm. from the garden. When a piece of the garden of a colony of Myrmicocrypta ednaella was placed in the nest nine Sericomyrmex workers immediately clustered about it as it lay against their own garden. They then dismembered it, at first dragging the pieces to one side, then later taking them all to a refuse heap. The *Megalomyrmex* workers came up and explored the pieces but took no part in the removal.

As Dr. Wheeler noted, the guest ants are very much quicker and more agile than the deliberate, slow-moving Sericomyrmex. The two also contrast sharply in appearance, the guest ants being a shiny, sleek brown with few hairs, they host being angular and dull-colored to the naked eye.

The stomach of a basilisk lizard (Basiliscus basiliscus (L.)) from Miraflores, Panama, contained a female of this species.

### Trachymyrmer isthmicus Santschi (Plate 12)

This species was described in 1931 (Santschi, 1931) on the basis of two workers from Barro Colorado sent by Dr. G. C. Wheeler for determination. No other records of this species have been published nor any information on its habits or nest.

This species is evidently widely distributed on the island as my records from Va Tine, Snyder-Molino and Shannon trails would indicate. The nest entrance may be surrounded by the customary crater or this may be erected in the form of a friable turret. The nest chamber is buried in a few centimeters in the soil and the fungus garden resembles that of the typical attine. Like the average attine, it is not averse to nesting in the vicinity of other species of this tribe and I found one nest 10 cm. from a nest of Myrmicocrypta ednaella. Cyphomyrmex rimosus workers were foraging freely about both.

A colony of this species revealed a hitherto unknown habit which may be of general occurrence among Attini, a moving of the entire nest contents, piece by piece, from one site to another, evidently in response to a change in the environment.

June 22 at 10:50 of a rainless but alternately bright and part cloudy morning workers were discovered on the steep clay slope just below the second hundred meter post of Shannon trail. Each worker traveling westwardly was carrying a load and each one marching eastwardly was empty-handed, or rather empty-jawed, since only the mandibles are used by ants for carrying objects. Closer examination revealed that

these loads were definitely fragments of a fungus garden and that I had stumbled upon an attine migration.

From 10:50 to 11:55 this migration was continuously watched. Not only were the ants carrying the fungus garden but also larvae which were covered with a mycelium, a common condition among Attini; one ant carried a piece of insect feces. As many as five workers would be seen at one time carrying loads. All were marching between two holes which were separated by 37 cm. in a direct line but the path the ants took over two large roots, a number of leaves and their own crater, when measured with a chain was 52 cm. The holes were 6 mm. in diameter and obviously 6 mm. was the maximum width of the object which could be removed. The hole to which the ants carried loads was bordered by a semicircular crater 6 cm. high and 11 cm. in maximum diameter over which the ants crawled. This hole was at a slightly higher level than the other, the latter being in a slight depression among the roots. The volume of material carried by each ant was from twice to five times that of its head. Four consecutive workers were checked for the time necessary to come out of the old entrance and carry the load to the new entrance with the following results in seconds: 65, 67, 80, 63, an average of 69 seconds. During this period a worker Ectatomma ruidum came up, took a position 10 mm. the line of march on the crate slope and «froze» but did not interfere. It eventually moved off, evidently not detecting any available prey or piece of food. Six workers were above ground carrying loads at 11:02. From 11:07 to 11:17 22 workers left the old nest with loads for the new, an average of 2.2 workers per minute. One worker returned to the old nest with a piece of dead leaf. In a five-minute period, 11:35 - 11:40, the following twelve ants came out with loads: 1st minute — one ant; 2nd minute — no ants; 3rd minute five ants close together; 5th minute — two ants. One worker went down the old entrance with a piece of dead leaf. The rate 2.2 ants per minute by coincidence is exactly that of the earlier period but in neither period did the ants come out at regular intervals. When I picked up one worker with its load of fungus-garden the ant dropped it near the trail but another came along soon, promptly picked the load up and took it down the new entrance.

At 2:45 p.m. the ants were still carrying pieces of the

fungus garden, the afternoon being bright, clear and hot. In a ten-minute period (2:45 - 2:55) only seven carried loads to the new nest while fourteen returned empty-jawed to the old crater. At this time it thundered intermittently overhead. At 3 p.m. four workers were timed between nest entrances as in the morning with the following results in seconds: 70, 80, 51, 71, an average of 68 seconds for the time taken to traverse the 52 cm. path. This compares closely with the 69 second period in the morning. Both in the morning and in the afternoon it was noticed that the ants did not follow exactly the same path; the deviations, however, were usually but a fraction of a centimeter and so unimportant. When one worker would deviate slightly the following ant would sometimes, but not always, follow it. This would indicate that it is not only «memory» but the chemoreceptors which enable an ant to follow a trail, each ant leaving an odor which the following ant picks up. Where a trail is followed by many ants such a strong odor trail is laid down that the individual ant variations from the path are only occasionally followed and it is easy for an ant to get back on the trail. The area covered by the trail was not physically altered to the human eye.

Since in the afternoon a perceptible number of empty-jawed ants were returning to the old nest I timed the return speed for four consecutive ants with the following results in seconds: 56, 51, 66, 55, an average of 57 seconds. Both the 51 sec. and the 55 sec. ants stopped momentarily to exchange antennal caresses with two laden and one unladen ants. The ants sped up noticeably when they crossed the even expanse of a dead leaf in the middle of the path.

Ants were still carrying loads at 4:05 p.m. The next morning, June 23, between 8:30 and 9:30 there was no sign of activity. The crater had been somewhat beaten down by the rain at night. The morning was partly cloudy and the humidity very high. During the afternoon 2.5 inches of rain fell.

June 24, 11 a.m. no ants were out. The morning was partly cloudy but no rain fell. All evidence of a crater was washed away by the previous day's heavy rain. Both entrances were open. Several workers appeared at the entrance to the new nest but there was no activity outside either entrance. At 11:10 four or five workers, milling about in the new en-

trance, came slowly out and explored the vicinity of the nest. At 11:12 one went down the old entrance. At 11:14 a worker came out of the old entrance with a burden of fungus garden which it took to the new entrance. At 11:17 another came out of the old entrance with a similar load; several ants from the new entrance went down the old entrance. At 11:26 a worker came out of the old entrance, explored the surface within a radius of about 2.5 cm., then picked up what seemed to be a pellet of clay twice its head size and went down the same entrance. Random actions of this nature have frequently been watched in ant colonies. From 11:10 to 11:34 only two loads of fungus garden were transferred. From 11:25 to 11:32.5 a worker from the old entrance tugged on a small section of yellowed dead leaf stem three centimeters from the entrance. When the stem finally came loose from the soil the ant carried it directly to the new entrance, taking 1.5 minutes for the trip. During the afternoon and evening 1.28 inches of rain fell, thus stopping all activity above ground.

June 25 at 11:15 a.m. the old entrance was found to be still blocked up by the June 24 rain. The shallow depression in which it stood had been partly scoured and partly filled with debris by the water running down the slope. A fallen leaf partly covered the new entrance but several ants could be seen at the entrance. At 9:30 p.m. in the clear evening both holes were blocked up with soil, evidently by the ants, since no rain fell all day. No soil had been carried out from either entrance and the ants had probably been occupied all day with rearranging the fungus garden in the new nest.

On June 26 at 2:45 p.m. there was still no sign of the old entrance and occasionally at the new entrance workers clustered without coming above ground. The day was clear and no rain had fallen since June 24. No excavating had been done as indicated by the lack of a crater or soil grains in the vicnity.

On June 27, 0.11 inches of rain fell in the morning. The afternoon was overcast. At 4:45 p.m. the ants were found to have opened the old entrance. At the new entrance two workers could be seen. No activity was seen above ground and no ants were visible in the old entrance.

No further observations could be made until August 13 because of a trip to Colombia.

On August 13 there was no sign of the old entrance and rains had washed away what crater may have been built around the new entrance so that only the bare entrance remained.

The history of this migration may be reconstructed as follows:

This colony of ants probably nested successfully during the preceding dry season, and perhaps for a longer period, in a slight depression on this steep clay clope. During the seven-day period, June 14-20, inclusive, 8.40 inches of rain fell and this depression became water-soaked, inundating the nest or at least soaking the walls of the chamber and wetting the garden. June 21 was a rainless day and the ants started to move the fungus garden and brood to a higher, less water-soaked situation. When I found the nest on June 22 the moving was well underway. By the morning of June 24 the entire nest had been moved. Three days were thus probably consumed in moving. Assuming for rough purposes of calculation that the ants worked steadily the entire time and that 2.2 trips per minute represented an average number, the total number of trips in the 72 hours would be of the order of magnitude of 10,000.

## Trachymyrmex cornetzi Forel ssp. gatun Weber

Santschi (1931) has described and illustrated a single worker from France Field, Panama, as T. uncifer whose description and illustration differs in many respects from my Barro Colorado ants, which I have described as a cornetzi subspecies. Though he does not compare uncifer with any other ant it is possible that the two forms are more closely related than a description based upon a single specimen would indicate. My specimens agree well with those which I have taken in Trinidad, British Guiana and Colombia, which are clearly referable to cornetzi or its subspecies bivittatus, except for subspecific differences.

This form is widely distributed on Barro Colorado and I have taken it in the vicinity of the laboratory and Snyder-Molino, Shannon, Fairchild (No. 11), and Wheeler (nos. 7 and 9) trails. In a hike along the entire length of Fairchild trail June 21 a worker of this form was the only attine seen (at No. 11) though I looked briefly for them in many places. In August, however, I found ants belonging to several attine species at the beginning, and a colony of Acromyrmex echinatior at the end of this trail.

Two nests were found, one June 12, and the other August 13. Both had crater nests of typical attine construction. The June nest had a crater 60 mm. high, 90 mm. in maximum diameter and a nest opening 3 mm. in diameter. The fungus garden was in a cell at a depth of 70 mm. whose diameter was about 50 mm. The ants were somewhat quicker in their movements than is common in *Trachymyrmex*. One worker was seen carrying in unrecognizable black vegetal matter. The August nest was 30 cm. from a nest of *Myrmicocrypta ednaella*. The *Trachymyrmex* crater was 25 mm. high at a depth of 40 mm. The fungus garden was found in a cell 35 mm. high by 25 mm. in diameter. The garden was bluishgray externally, yellowish-brown internally. A lone female was taken by Dr. E. C. Williams, Jr., on July 19 and I found another female June 13 walking on a fallen leaf.

These ants use caterpillar feces and vegetal debris for substrate and one worker was seen carrying a piece of a flower to its nest close by an old French dump cart used in work on the Canal years ago. One worker was seen foraging close to a nest of *T. morgani*. Where gatun workers were carrying out sand grains from their nest a worker of Aphaenogaster (Deromyrma) was watched. Several times it ran quickly up to the attine workers, as if to snatch their loads, only to retreat without encounter. Perhaps if the attines had been carrying insect remains they would have been startled into dropping them to the advantage of the robber Deromyrma. The phlegmatic attines, however, kept on with their work.

## Trachymyrmex morgani Weber (Plate 11)

This new species, which I have dedicated to the buccaneer who sacked Old Panama, is so small (2mm.) and inconspicuous as to be easily overlooked. I found it on three occasions near Snyder-Molino and the beginning of Shannon trails but it undoubtedly is more widespread on the island and the Isthmus. Like the other related small species, it is probably locally distributed and comparatively rare. Several workers were detected coming out of a hole 3 mm. in diameter in a vertical wall on the clay ridge up which Snyder-Molino trail extends. These ants were moving about slowly. If this was the nest entrance, rains had probably washed any turret or crater entrance at this steep and comparatively exposed place.

A nest found June 22 on a very steep slope with a northwest exposure was surmounted by a turret of fine clay grains 21 mm. high and 11 mm. thick which leaned downward at an angle of about 10° from the perpendicular. From an opening 4 mm. in diameter a tunnel led about 60 mm. to the nest chamber. The chamber was lens-shaped with the long axis perpendicular instead of horizontal as in most Attini. The diameter was about 30 mm. and the width about 20 mm. Five holes pierced this chamber and may have represented entrances to the outside which had been filled by the wash of clay down the slope or may have represented the beginnings of accessory chambers. The grayish fungus garden, irregular in shape but nearly filling the chamber, was suspended on rootlets piercing the chamber. It was noteworthy in that the bromatia were unusually compact and suggested the cheese-like bromatia of Cyphomyrmex rimosus. A scanty mycelium, however, covered the substrate and such a mycelium is lacking in C. rimosus.

### Trachymyrmer zeteki Weber

This species is dedicated to Mr. James Zetek, who has taken such excellent care of the island. The workers from which it is described were taken from their nest on the steep hill in dense shade. The nest was accidentally discovered June 13 in digging a hole back of the laboratory and was damaged before extensive observations could be made. The single chamber of the nest was at a depth of about 67 mm. and was horizontally elliptical, 42 mm. high by 80 mm. wide. The fungus garden, only slightly smaller than the nest chamber, was of typical attine appearance.

A single worker was taken June 25 while it was foraging over the forest floor near Snyder-Molino trail at 9 p.m.

### Trachymyrmex balboai Weber

This new species is dedicated to Balboa, the discoverer of the Pacific Ocean. The workers from which it is described were taken on a steep hillside just above a stream on Barro Colorado. From a hole  $15\times7$  mm. in the steep bank at a point immediately below a horizontal root the ants carried soil 16 cm. away to form a crater,  $11\times19$  cm., to one side and slightly below the entrance. Workers were busily en-

gaged in excavating, as many as 15 being out of the nest at one time. Each worker leaving the nest carried a glistening pellet of tan clay as large as its head to  $1\ 1/2$  times larger. There was unfortunately no time to excavate the nest. A worker taken at Wheeler 9 trail was at the entrance  $(12\times7\ \text{mm.})$  to its nest. The crater to the nest was about 10 cm. away. A stray worker found walking on the forest floor at 9 p.m. is the only other record of this species.

### Acromyrmex octospinosus Reich ssp. echinatior Forel (Plate 13)

This is the only Acromyrmex recorded from Barro Colorado. Acromyrmex is found throughout the American tropics from Arizona to Argentina and many forms have been described. The subspecies octospinosus has a wide range, including the Guianas, Trinidad and Venezuela, while the subspecies echinatior is known from Mexico to Rio Frio, Colombia and Guayaquil, Equador. Many species, especially of the subgenus Moellerius, have invaded grasslands and cultivations but as a whole this is a forest genus. I have found the subspecies octospinosus nesting in such diverse places as 14 ft. up in the crown of a palm in the Port of Spain Botanical Gardens, Trinidad, and in debris about the base of a clump of palms barely above high tide level in the swamps of the Orinoco Delta. The members of this genus are second only to the Attas in conspicuousness of their leafcutting activities. They may readily be told from Attas by the absence of a large soldier caste, the tuberculate as well as spinose integument which is dull instead of shining, and by the stouter habitus. The trails never are as broad and populous as a welldeveloped Atta trail.

Echinatior nests on Barro Colorado in the unbroken rain forest and is probably found in all parts of the island. The nest figured (Plate 13) way found August 15 on the rocky slopes close to Barbour trail near the fifth hundred meter post in a well-drained situation under a small, angular rock. The fungus garden, pale yellow in color, was 10 cm. in greatest diameter and 3.7 cm. deep, It rested on small, angular fragments of rock upon the ground and no excavation had been made. Close to the garden was a pile of exhausted substrate 3.5 cm. long, 1.5 cm. wide and 1.5 cm. deep which was of a yellowish brown color. 46 cm. from the garden was a

small nest of Apterostigma angulatum, also on small rock fragments. Such a situation for these nests insured a nearly constant environment. Investigations of Allee (1926) and others have shown that in the dense rain forest shade relative humidity on the forest floor is nearly constant, daily and seasonal, while the temperature likewise varies only slightly. This rocky slope was well shaded and only small, transitory patches of sunlight would fall upon the rocks, too ephemeral to heat them. The fungus gardens, being suspended on rock fragments under larger rocks, were well protected from any tendency of torrential downpours to wash them away.

In this nest workers, brood and a single queen were present. From the circunstance that single, dealate females June 10 and June 14 were found crawling by themselves under leaves one would suppose that they had but recently lost their wings after a marriage or dispersal flight, at which time males would also emerge. Mature males and virgin females thus may be expected to be found in nests in May or nearly June. The onset of the rainy season at this time is probably the stimulus that leads them to take flight. This is in accord with my findings in Trinidad concerning the subspecies octospinosus.

Visitors to Barro Colorado may observe an amusing habit of this ant if they will take a flashlight on a calm night and look in the vicinity of the cook shack back of the laboratory. More than once in June and in August I found long files of workers pillaging the garbage can and its vicinity for what starchy food, particularly bread, had been left by an active troop of coati mundi and the semi-tame female deer which hung about the clearing. Each worker would take a piece several times the size of its head firmly in its mandibles and march off, with the piece held erect above the thorax, to the edge of the clearing. This mischievous habit frequently arouses the ire of cooks and storekeepers as I have more than once observed. A worker in the British Guiana goldfields, held responsible for a cache of supplies at a temporary depot, was nonplussed at the melting away of the store of rice, split peas and soda crackers (biscuits). At the time of my visit the cause was readily explained. A long army of workers of Acromyrmex coronatus andicola globoculis Forel were filing out from under the log floor of the hut, each carrying a large piece of cracker.

### Atta columbica Guér. var. tonsipes Santschi

This variety has been known only from the original discription based on specimens from Bellavista, Agua Clara, and Colon, Panama. I found it on Barro Colorado and also nesting on a slight knoll in the wet savannahs near Juan Diaz on the Pacific side of Panama as well as in Marsh's Zoo near the ruins of Old Panama. It may well be a savannah form which originally occupied the lowlands before Gatun Lake was formed and hence may not be a form strictly endemic to Barro Colorado.

A nest at the end of the F. Drayton Trail was found in the heavy Heliconium growth just back of Termite House. At 9 a.m. of an overcast morning workers, mostly media, were marching in large numbers, with much regularity in the file, to a point under the house but there was unfortunately no time for other observations. The Juan Diaz nest was in lush grass and part of the nest was beneath a large, long dead and whitened, tree trunk. No distinct craters were seen, but one large tunnel extended more than a foot under the tree. At the time of the brief visit in the middle of a hot, sunny morning the numerous workers were cutting leaves of herbs and bushes. Similarly at Marsh's outdoor Zoo, thousands of workers at midday in the bright, hot sun were cutting leaf sections from the trees in the Zoo. I was told that they carried off corn and other food given to the birds in the outdoor cages. The workers formed dense, continuous files marching over the floors of the various cages, ignoring birds, cats rodents and other animals. The stomach of a basilisk lizard (Basiliscus basiliscus (L.)) from Rio Indio, Gatun, Panama, in the Field Museum contained workers of this ant.

### Atta cephalotes L. isthmicola, ssp. nov.

The common Atta of Barro Colorado has been identified as both the typical Atta cephalotes and as A. cephalotes polita Emery (Allee, 1926; Lutz, 1929). A. polita is regarded as a well-defined species found from Bolivia south; the Barro Colorado form obviously belongs to cephalotes and has remained undescribed.

The female differs from typical cephalotes chiefly in having shorter and sparser pilosity so that the body appears smoother, the elongate brown blotch on the gaster more distinct, and the sculpturing of the head feebler. The soldiers are polymorphic (about 9-13 mm. long; thorax length 4.1-5.4 mm.), have the hairs of the front part of the head extending higher than in *cephalotes* and the occiput more densely and deeply punctate except on the sides so they seem less «bald-headed». Media and minima workers have a much shinier integument, darker thorax, and more curved anterior thoracic and epinotal spines than cotypes of the variety *erecta* Santschi of Costa Rica; their thoraces are darker than those of typical *cephalotes* and contrast more with the paler head and thorax.

Holotype female and cotype workers are from one colony (N.º 753) which I collected June 12, 1938 on Barro Colorado Island just off Snyder-Molino trail at N.º 1 post.

Atta cephalotes and A sexdens are two of the economically most important ants in the world. Their depredations on agriculture have made necessary detailed studies with a view towards their control, particularly in Mexico and Brazil. Generally speaking, A. cephalotes occupies the northern half and sexdens the southern half of the continental New World Tropics though their ranges overlap in the Guianas and elsewhere. The other species are more limited in distribution.

A. cephalotes isthmicola is distributed generally over Barro Colorado and the files of workers carrying sections of leaves are often to be seen. They frequently follow well-defined trails for many yards and also follow raised logs and branches near the ground, thus avoiding obstacles. Not only do they carry green leaf and fresh flower sections but sometimes dead and discolored parts of leaves. Such a habit was exhibited by a file of workers June 10. These were carrying dead leaves which were quite wet from rain falling an hour or so before.

June 12 a file of workers was climbing the smooth gray back of a tree to a height of fully 12 meters to some of the outer branches of the crown. Here they cut sections of the acuminate-ovate smooth leaves, frequently leaving only the larger veins of the leaves. It was 63 meters from the tree to the base of the ant nest. Only the workers of medium size were engaged in leaf-cutting. One solitary worker was found two meters above ground on top of a rotted branch of another tree 2.5 meters away. It was alone and had evidently fallen down from the tree being stripped. Two of the numerous fungus gardens of the nest were exposed, each at a depth of about 20 cm. They were about 20 cm in diameter, suspended on numerous roots, and were gray externally, yellowish



Nest of Cyphomyrmex rimosus Spinola as it appeared when the overlying log was removed. In the irregular chambers (center) appears the fungus garden of insect feces with cheese-like tiny masses of bromatia peculiar to this widespread species. (Barro Colorado Island, N. A. Weber photo)



Cyphomyrmex costatus Mann nest on left which contained a colony of the new guest ant, Megalomyrmex wheeler; Weber. The latter colony was in an earth cell which opened only to the single fungus garden of the host. Gray patch on right the young fungus garden of Apterostigma mayri Forel. Forel.

Forceps 113 mm. long. (Barro Colorado Island, N. A. Weber photo)



Crater entrance to nest of Mycocepurus tardus Weber to left of 113 mm. forceps. Several openings lead to the single tunnel which in turn leads to the fungus garden in the soil several centimeters below the surface. (Barro Colorado Island, N. A. Weber photo)



Irragular crater entrance to nest of Myrmicocrypta ednacla Mann. Several centimeters below the surface was the single large fungus garden. (Barro Colorado Island, N. A. Weber photo)



Nest of Myrn.icocryn ta ednaella Mann. Folceps (113 mm. long) point to nest entrance beneath which is the single fungus garden. (Barro Colorado Island, N. A. Weber photo)



Polydomous nest of Apterostigma angulatum Weber in a crevice in the soil. The crevice had been against a boulder which had rolled down a steep slope. Beneath the 15 cm. ruler appear two fungus gardens and there was another on each side (Barro Colorado Island, N. A. Weber photo)



Fungus garden of Apterostigma angulatum Weber clinging to the under surface of a log as it appeared when the log was overturned. The garden funded into a symmetrical cell in the soil. Steel tape ruled in half-centimeters. (Barro Colorado Island, N. A. Weber photo)



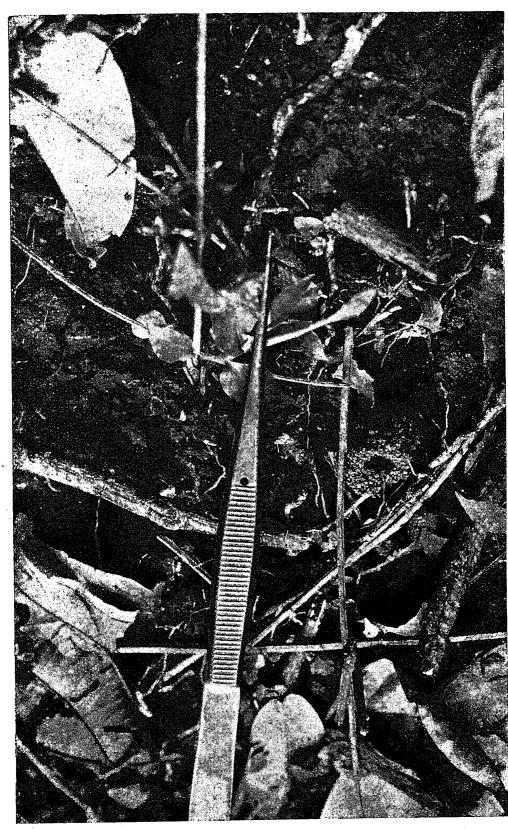
Close-up view of the garden of Apterostigma angulatum on Plate 7. The entire garden was covered by a silk-like mycelial envelope except for two openings on the right. (Barro Colorado Island, N. A. Weber photo)



Close-up view of the garden of Apterostigma angulatum on Plate 7, as it appeared when the ventral part of the envelope was removed. Loosely cellular fungus garden contained the brood and adult ants. (Barro Colorado Island, N. A. Weber photo)



Nest of Sericomyrmex amabilis Wheeler which contained a colony of the guest ant, Megalomyrmex symmetochus Wheeler. The latter colony occupied the lower part of the fungus garden of the host. Steel tape ruled in half-centimeters. (Barro Colorado Island, N. A. Weber photo)



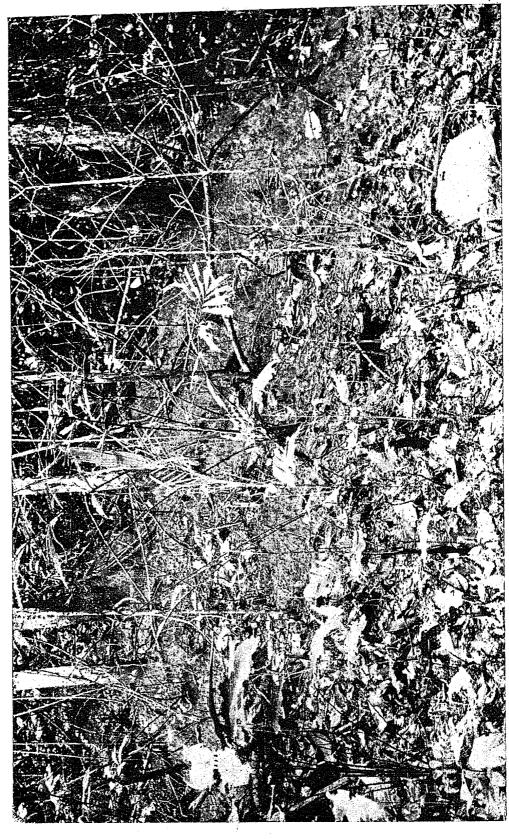
Crater entrance to nest of Truchymyrmes: morgani Weber, one of the smallest species of the genus. Forceps 113 mm. long. (Barro Colorado Island, N. A. Weber photo)



Site of the nest-moving of a colony of Trachymyrian isthmicas Santschi. Entrance of the old nest at the tip of the forceps (which are 113 mm. long). Crater entrance to the new nest in upp right. Path taken by the ants in carrying fungus garden and brood to new site 52 cm. long. (Barro Colorado Island, N. A. Weber photo)



Nest of Acromyrmax octospinosus colunation Forel (lower right), containing a single fungus garden as it appeared when the overlying rock was removed. The rock also covered the small nest of Apterostigma angulatum Weber (upper left). (Barro Colorado Island, N. A. Weber photo)



Large multiple-crater nest of Atta cephalctes subsp. isthmicola Weber on a moderate slope. By persistent defoliation the ants had formed a clearing about the nest. Partly defoliated small palms and saplings in foreground. (Barro Colorado Island, N. A. Weber photo)

brown internally. Bromatia were abundant on both gray and brown parts. A single queen was found in one of the gardens.

A large nest is to be found on a moderate slope at R. C. Shannon trail at No. 11. This nest, on June 23, was 6 meters wide at the base, following the contour of the slope, and extended 10.5 meters up the slope. The base was close to a pile of old French wine bottles left from the French attempt at digging the Panama Canal. Extending in this direction and beneath the human trail was a small tunnel which was uncovered in four places of small area. The workers were traveling in this tunnel all morning although no ants were to be seen above ground except at the highest crater, where a few minima workers were bringing up soil particles. Rain had beaten down many leaf sections about the nest. Many were dead and black but there were some freshly green. These had doubtless been beaten down by rain which fell from 8:30 to 9:30 the previous evening. My observations in British Guiana and Trinidad (Weber, 1937b) on the responsibility of the ants for the clearing commonly found about long-established nests of cephalotes were strikingly confirmed here. Three saplings on the nest 2.5, 2.3 and 2.2 meters, respectively, in height were completely defoliated. A young palm 1.7 meters high was partly defoliated as were numerous saplings. The persistent defoliation of the young trees growing over the nest in all probability eventually kills them. The larger trees are not importantly harmed and persist unless the aeration at their roots in time causes damage.

When the nest was revisited June 26, 4:30-5 p.m., the ants were not active above the nest though a few were

	Trinidad, etc., cephalotes	Barro Colorado cephalotes isthmicola
Habitat	forest	forest
Soil preference	clay	probably clay
Shape of nest	multiple crater	multiple crater
Depth of first gardens	shallow	shallow
Size of gardens	large (about 25 cm)	smaller (about 20 cm)
Appearance of garden	quite uniformly gray-	gray outside, yellowish-
	brown	brown inside
Workers	aggressive	aggressive
Polymorphism of sol-	slight	marked
diers		
Soldiers	easily provoked from nest	reluctant to leave nest

traversing the tunnel beneath the human trail. Withered green leaf sections on the nest showed that they had been active the previous night in leaf-cutting. Those sections that had been dropped around the nest entrances obviously had been there all day.

The table on page 129 compares the Barro Colorado cephalotes isthmicola with the cephalotes found in Trinidad, the Orinoco Delta in Venezuela and British Guiana.

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